University of Alberta

Partial cutting impacts on moths and lepidopteran defoliators in a boreal mixedwood forest of Alberta.

by

Louis Morneau ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **Master of Science**

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To my wife, Josée, for her love and ever-present support and to my parents,

Claire and Jean, for teaching me important values.

Abstract

A boreal lepidopteran community was assessed by whole-season light trapping for moths and whole-tree sampling for defoliators of aspen and spruce canopies in northern Alberta, Canada, before and immediately after logging with two different levels of green-tree retention. Partial cutting significantly decreased both moth trap catch and species richness, particularly of forest interior species, while generalist and pioneer plant feeder species increased in abundance. The larval community differed considerably between aspen and spruce canopies, yet was dominated by tortricid pests [*Choristoneura conflictana* (Clem.) on aspen and *Choristoneura fumiferana* (Clem.) and *Zeiraphera unfortunana* Powell on spruce] and one geometrid, *Operophtera bruceata* (Hulst), on aspen. Partial cutting showed potential for pest management as both spruce species investigated were less numerous per tree as the green-tree retention decreased. Post-harvest conservation of many forest species due to higher stand structure and plant diversity should increase biodiversity, at least for Lepidoptera, in the long-term.

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List of Abbreviations

ANOVA – Analysis of Variance

EMEND – Ecosystem Management by Emulating Natural Disturbance

NMS – Non-metric Multidimensional Scaling

RSC – Residual Structure Compartment

Chapter 1

Introduction

1.1 Biodiversity concerns

In Alberta, the forest industry greatly depends on the boreal mixedwood forest covering nearly two thirds of the province (Natural Resources Canada 1999). As more than 40,000 jobs are related to this sector of activity there are strong economic incentives to grow and harvest timber. Economic development has been planned and is occurring, however, without much action taken toward the conservation of forest biota. Forest companies are now planning to manage on an ecological basis for sustainability as recommended in the Canadian Biodiversity Strategy released in 1995. Nonetheless, ever-increasing demand for wood fibre prompts fear that short-term economic goals may still outweigh concerns about the integrity of biotic communities that characterize the pre-industrial boreal forest. We have insufficient understanding of these communities to anticipate the consequences of particular management approaches.

Indeed, interactions between the different biotic components, particularly those involving the invertebrate assemblages, are not yet fully understood. Insect diversity, for example, is still being updated significantly, even in Canada, because invertebrates are such a large group and difficult to quantify (Danks and Footit 1989). According to broad estimates, fewer than 800,000 species of

insects have been described from a possible much-debated total of 5 to 30 million worldwide (Erwin 1982; May 1988; Gaston 1991; Stork 1993).

1.2 Lepidopterans as indicators of disturbance

Invertebrates play key functional roles in forest ecosystems, such as in contributions to forest litter decomposition and nutrient cycling (Seastedt and Crossley 1984). As phytophagous insects, they also play an important role in regulating forest primary production (Mattson and Addy 1975; Schowalter 1985). Many major forest pests responsible for major wood fibre losses in the western boreal forest belong to the order Lepidoptera (Volney and Mallet 1998). These include the forest tent caterpillar (*Malacosoma disstria* Hubner), spruce budworm (*Choristoneura fumiferana* (Morris), large aspen tortrix (*Choristoneura conflictana* Walker) and Bruce spanworm (*Operophtera bruceata* (Hulst)). Populations of these species have an impact on ecosystem function by changing both the vertical distribution of biomass and the plant community composition (references in Schowalter *et al.* 1986).

Furthermore, Lepidoptera have excellent potential as ecological indicators (Holloway and Stork 1991; Kremen 1992a, 1992b), because they are taxonomically well described, well studied ecologically and known to be important in forest food webs, easily sampled, diverse and numerous (Spitzer *et al.* 1996; see McGeoch 1998 for an overview). As is the case for many arthropods (Spence *et al.* 1996; Buddle *et al.* 2000), lepidopterans are also

considered good indicators of disturbance as they quickly react to small changes in their environment (Kremen *et al.* 1993). Indeed, recent studies have shown that they are sensitive to disturbance (Warren and Key 1991; Holloway *et al.* 1992; Daily and Ehrlich, 1996; Hamer *et al.* 1997; Spitzer *et al.* 1997), partly because many species are constrained to a narrow range of food plants (Murphy and Wilcox 1986; Schowalter 1986). However, forest harvesting impacts on lepidopterans are not yet fully understood. Few studies of whole lepidopteran communities have been done in the boreal mixedwood forest, especially on non-outbreaking species (Danks and Footit 1989) which include the greatest number of Lepidoptera species (Hunter 1991).

1.3 Forest management issues

Forest practices have been changing significantly in Alberta over the last couple of decades (Lieffers and Beck 1994). As forest companies move toward ecosystem management, there is renewed interest in maintaining and creating mixedwood stands. Stands of mixed composition and structure promote ecological diversity and other benefits such as improved long-term soil fertility, reduced susceptibility to pests (Franklin *et al.* 1989), increased productivity (Lieffers *et al.* 1999) and improved economic yield (Burkhart and Tham 1992). Green-tree retention on clearcuts has also been implemented as a component of forest practices to maintain biodiversity by preserving natural processes and emulating critical aspects of natural disturbances such as wild fire (Angelstam

1997, 1998). However alternatives to clear-cutting in mixed stands (Lieffers *et al.* 1996) have been developed without much knowledge of defoliators in these systems although recent studies suggest that thinning has a lesser effect on forest fauna and flora than clearcutting (Niemelä 1999).

The major immediate impact of forest harvesting on Lepidoptera is removal of potential habitat. Partial cutting can change species assemblages often reflecting the invasion of residual stands by common generalist species and the disappearance of site-specific, old-growth specialist species (Kitahara and Fujii 1994). As for most insects, lepidopterans are microhabitat specialists with different species requiring different habitats, ranging from open space to old-growth forest stands (Roberts 1996), and several additional key components such as nectar-source plants or pools of standing water (Murphy and Wilcox 1986). Therefore it is reasonable to expect that the lepidopteran community will reflect changes in ecosystem integrity following disturbance.

This study proposes to evaluate harvest-induced changes in a boreal lepidopteran assemblage experimentally in the context of the EMEND (Ecosystem Management by Emulating Natural Disturbance) project framework (Spence *et al.* 1999). EMEND is a large-scale multi-disciplinary harvest-silviculture experiment in the boreal mixedwood forest of Alberta, Canada. The project investigates the costs and benefits of green-tree retention on harvested blocks as an approach to maintain the main ecosystem dynamics characteristic of forests driven by natural disturbance such as wildfire.

1.4 Thesis Objectives

In this thesis, I investigate the impacts of two intensities of partial cutting, seen as alternatives to traditional clear-cutting, in three different forest types on numbers, diversity and species assemblage of Lepidoptera, both in their adult (i.e. moth) and larval (i.e. caterpillar) life-cycle stages.

Chapter 2 deals with the impacts of three levels of green-tree retention (20%, 50% and 100%) on moth assemblages as explored through light trapping. First, I ask whether samples of captured moths differ between forest types and years, in undisturbed forest. Second, I seek to define the impact of partial cutting treatment on these moths and ask if late-season species are more affected than early-season species, reflecting differences in their developmental patterns. I predicted the existence of differences in terms of species assemblages and relative abundance between forest types, years, developmental patterns and treatments. These should reflect differences in plant community from one forest type to another (Magurran 1985; Waring 1989; Robinson and Tuck 1993), yearly variation in moth populations (Rejmánek and Spitzer 1982), life-cycles particular to each species (Young 1997) and stand-level changes in environmental conditions following harvest (Safranyik *et al.* 1998). Specialist species should be most affected by changes in the availability of larval food plants (Waring 1989; Woiwod and Stewart 1990; Kitahara and Fujii 1994) because larvae of many species are restricted to a narrow range of hosts (Handfield *et al.* 1999). For example, the poplar catkin moth, *Anathix*

puta (G. & R.) will rarely occur in the middle of pure white spruce (*Picea glauca* (Moench) Voss) stands where food plants well suited for development of its larvae are absent. I tested for these differences by comparing moths from light trap catches before and immediately after disturbance in different forest types and treatments.

In chapter 3, I examine defoliator populations in trembling aspen and white spruce canopies of pure and mixed stands with a focus on pest species. I ask if canopy trees of these two species harbor a different assemblage of defoliator species and whether thinning associated with partial cuts strongly impacts immature lepidopterans in both situations. I predicted that larval assemblages would differ conspicuously between aspen and spruce (Ives and Wong 1988), and that thinning would have an immediate impact on defoliators following thinning (Bauce 1996). I tested for differences by assessing defoliator assemblages, numbers, and diversity in trembling aspen and white spruce canopies in stands subjected to two intensities of partial cutting (20% and 50% residual structure) and unharvested stands.

Finally, in chapter 4 I summarize and discuss the management implications and importance of my findings. I also place them in the context of other relevant work pertaining to human disturbance, forest management and biodiversity preservation and renewal.

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Chapter 2

Partial cutting impacts on a moth community

2.1 Synopsis

A boreal lepidopteran community was assessed by whole-season light trapping in northern Alberta before and immediately after logging (1998 to 2000) with two different levels of green-tree retention aimed at preserving forest species. Analysis of variance, non-metric multidimensional scaling, and indicator species analysis are used to compare moth assemblages among logging treatments (20, 50 and 100% of trees left on site) and forest types (deciduous dominated, deciduous with a spruce understory and conifer dominated) in terms of diversity, abundance, habitat use, seasonal pattern, host-plant range and feeding guild. Assemblages were similar across forest types and dominated by habitat use generalists and polyphagous species. Partial cutting resulted in significant decreases in both moth trap catch and species richness. Moth populations from some families responded differently, possibly reflecting structural features that characterize moths within a family. Logging treatments negatively affected trap catch of Noctuidae, Geometridae, Uraniidae and species richness of Geometridae and Notodontidae. Early- and late-season species assemblages differed considerably in composition but their respective responses to disturbance were similar. Finally, logging treatments increased abundance of generalist, grass and pioneer plant feeders but decreased abundance of deciduous tree, conifer, woody plant and lichen

feeders. I predict that moth assemblages will return to and possibly exceed pre-disturbance richness with time, as plants respond to partial cutting with an increase in their diversity. A long-term commitment to monitoring moth populations is required to determine the ultimate impacts of logging on arthropods.

2.2 Introduction

Biodiversity is now recognized, along with disturbance regime, species composition, soil type and climate, as a significant factor affecting ecosystem function (Tilman 1999, 2000). The processes allowing coexistence of interacting species in an ecosystem also influence system productivity, nutrient cycling and stability (Johnson *et al.* 1996). With increasing pressure from resource extraction industries, need has arisen for operational impact thresholds that will hold extraction within limits that maintain both biodiversity and long-term productivity of boreal forest ecosystems. Naeem (1998) has suggested that ecosystem function could be affected negatively by loss of particular species within certain functional groups. However, in the absence of perfect knowledge, the precautionary principle urges us to maintain biodiversity *per se* (Simberloff 1999).

Experiments to evaluate effects of disturbance may explore the responses of various potential indicator groups that will provide information to guide forest managers. Arthropod assemblages are generally considered good

indicators of disturbance because they are sensitive to small environmental changes and thus respond quickly to change (Kremen *et al.* 1993; Spence *et al.* 1996; Buddle *et al.* 2000). The insect order Lepidoptera, the moths and butterflies, which are diverse and numerous in northern forests, may be especially suitable as indicators of changes to forest systems. The night flying moths are increasingly well known both taxonomically and ecologically. They are abundant in boreal systems, quite easy to sample, and larval populations of many species are tightly linked to significant impacts on forest growth and yield (see review on criteria by McGeoch 1998). In the western boreal forest, wood fibre losses to insects are primarily caused by lepidopteran defoliators (Volney and Mallet 1998) and it has been suggested that these creatures could regulate forest primary production in the long term (Mattson and Addy 1975). Understanding the dynamics of this taxon at the community level is thus both significant as a contribution to understanding ecosystem processes and relevant to the other objectives of forest management.

The major immediate impact of forest harvesting on Lepidoptera is removal of potential habitat and reduction in amount and variety of larval food. In this study, I ask about the extent to which a moth assemblage characteristic of unharvested areas can be retained when varying amounts of forest structure within stands are removed by winter logging. This type of harvesting is widely used in western Canada, giving forest managers access to poorly drained areas when soil is frozen, thereby limiting soil disturbance (Zasada *et al.* 1987).

Forest habitat altered by logging might be used differently than undisturbed stands by Lepidoptera, which are highly mobile, flying organisms. Furthermore, habitat use by various moth species in the mixedwood forest can be contrasted among various cover types. Habitat use is defined here as the utilization of homogeneous forest compartments by moths to mate, lay eggs, nectar-feed on plants, take cover or simply to travel (Young 1997).

The immediate impact of logging should also differ between early- and late-season breeders. Early breeders will have spent the winter as pupae, will emerge in the spring and adults will be able to disperse to locate suitable larval habitat, even beyond the boundaries of a harvested stand. Late-season breeders, in contrast, will spend the winter as eggs or young larvae and depend immediately on the availability of suitable larval food within the stand. A portion of late-season breeders will be removed from a stand by logging and those left would be subjected to different environmental conditions affecting their development and survival.

Because Lepidoptera is a well-studied insect order, it is possible to study the moth community from different perspectives. The host-plant range relates to many aspects of moth biology and it should largely mediate disturbance impacts on lepidopterans. Most species in the same family share some common traits (feeding, body structure, and behavior). Thus, populations of a geometrid (external feeders as larvae, slender-bodied, broad-winged and rather delicate as adults with restricted mobility) are more likely to be negatively

affected to a severe removal of habitat (Scoble 1992) than those belonging to the Sphingidae (stout-bodied strong fliers). Also, families with feeding adults (e.g. Geometridae, Noctuidae) might be affected more than those with non-feeding adults (e.g. Lasiocampidae, Saturniidae) by the destruction of understory flowering plants (source of nectar) immediately following cutting.

The objectives of this project were to 1) assess and compare moth diversity in three different undisturbed forest types and to 2) investigate impacts on the moth community of forest harvesting with two levels of tree retention. These objectives were addressed by replicated light trap collections of moths from the same stands one year before and two years after disturbance by winter harvesting. Thus, the study focuses on the immediate impact of a disturbance on a biotic community.

The following hypotheses were tested:

1. Each forest type will have specialized moth species but will also share many common species.
2. Partial cutting will decrease moth species richness and trap catch compared to uncut sites and impact will vary with harvest level.
3. Moths from different families, habitat use groups, host-plant range groups and feeding guilds will respond differently to disturbance [e.g. populations of generalist herbivore species will increase after disturbance due to the establishment of early successional plant species

(Cates and Orians 1975) and a short-term increase in plant diversity following forest harvesting (Peltzer *et al.* 2000)].

4. Immediately following harvest, late-season breeders will be more negatively affected than early season breeders due to their developmental pattern.

2.3 Material and Methods

2.3.1 EMEND Site and Study Design

This project was executed under the umbrella of EMEND (Ecosystem Management by Emulating Natural Disturbance) (Spence *et al.* 1999), a large-scale multidisciplinary harvest-silviculture experiment in the boreal mixedwood forest of Alberta, 85 km northwest of Peace River (56°44'N, 118°20'W). The project investigates the costs and benefits of retaining residual green trees on harvested blocks as an approach to maintaining the main dynamics characteristic of ecosystems driven by natural disturbance such as wildfire. Different partial cutting levels were chosen to investigate commercial alternatives to clearcutting. The site is in the Lower Foothills natural subregion (Beckingham *et al.* 1996) of the Boreal Forest region (Rowe 1972) characterized by trembling aspen, *Populus tremuloides* Michaux, balsam poplar, *Populus balsamifera* L., white spruce, *Picea glauca* (Moench) Voss and black spruce, *Picea mariana* (Miller) B.S.P. (Johnson *et al.* 1995). Vegetation in

the area grows on fine-textured luvisolic soils (B. Kishchuk, personal communication).

Sites were selected from the 1998 EMEND treatment compartments (Figure 2.1) according to forest type, treatment type, compartment shape and accessibility. Each compartment was 8-10 hectares in size. Three forest types based on canopy composition were considered: deciduous dominated (>70% trembling aspen and balsam poplar), deciduous dominated (>70% trembling aspen and balsam poplar) with a strong white spruce understory 30-70% of canopy height, and conifer dominated (>70% conifer, mainly white spruce). Four of the seven EMEND treatments (Volney *et al.* 1999) were examined: partial cutting resulting in 20% and 50% residual structure compartments (RSC), a control to be used for prescribed burning in the near future, and an unharvested control. Each treatment was replicated twice within cover type for a total of 24 sites. Compartments selected for burning became a second set of unharvested controls in 1999 because conditions suitable for the prescribed burning had not yet materialized.

2.3.2 Sampling

The moth community was sampled with light traps (Bioquip, CA, USA), using 12 volt UV lights running on batteries and equipped with photoelectric detectors to activate the U-shaped bulbs. Trap deployment was standardized at a height of 2 meters on tripods, and photosensors were oriented north. The moth community was sampled before (1998) and after (1999 and 2000)

disturbance by logging during the winter of 1998-99. Trapping occurred every 8-10 days, depending on local weather conditions, from May to mid-September for a total of 14 trapping nights per year. Sixteen traps were used to sample 24 sites under a partial replication design employed to constrain the number of traps used any one night within manageable bounds. Replicate one consisted of twelve sites sampled every trapping night. Replicate two consisted of twelve sites, four of which were sampled on any trapping night. Thus, over three trapping nights, all cover types would be sampled twice, covering the range of forest types and treatments considered.

2.3.3 Environmental variables

Many factors are known to affect light trap catches, including temperature, humidity, wind, moonlight, proximity to vegetation, height of trap above ground, trap design and light source (Bowden 1982; Wallner *et al.* 1995; Young 1997). However, most of these factors were not considered in the analysis since they were similar at all sites on any given sampling night thus affecting each catch in the same way. Problems related to weather factors and trap design were overcome by standardizing sampling techniques and trapping nights. Only structural site factors were analyzed for potential effects on trap catch: basal area reflecting tree density and canopy cover after thinning, slope, and understory vegetation height. Understory vegetation density was also measured indirectly in a light interception experiment. A laser pointer was used at night to aim at the light trap bulb from 36 different points around a circle.

Binary data from the laser beam either reaching or not reaching the bulb were recorded. The experiment was repeated on circles of 5, 10 and 20-meters radii centered on the trap as moths response to light was estimated to be no more than 10 to 25 meters (Baker and Sadovy 1978).

2.3.4 Laboratory work

Moths were collected in paper bags the day following each trap run and frozen at the EMEND field laboratory before being processed. Moths were sorted to morphospecies based on external characters and genitalia dissection when needed. Identifications were done using up-to-date literature, the Canadian Forest Service arthropod collection at the Northern Forestry Centre (Edmonton, Alberta, Canada), and advice from fellow lepidopterists. Voucher specimens were deposited in the NoFC collection. Classification followed Hodges *et al.* (1983) and more recent publications (Handfield *et al.* 1999). Bowman's work on Alberta Lepidoptera (1951) was also consulted.

2.3.5 Classification of moths into habitat use classes

Species were classified based on trap catch in the following four categories of habitat use: generalist, deciduous specialist, coniferous specialist or unknown. Generalists were species using all cover types as habitat or, as defined by Andrén (1994), species that used several habitats in the landscape although they may differ in suitability. Generalists were found in large numbers on most sites, totalling 71% of the overall moth captures. Deciduous and conifer specialists (19% of the total catch) were species only or mostly found

where aspen and spruce, respectively, accounted for a large proportion of the forest stand. Lastly, species with fewer than twenty specimens captured were not abundant enough to be assigned to a habitat class and were placed in the unknown category (10% of captured moths). Data from two years (1998 and 1999) were used for the analyses of habitat use to investigate the immediate impact of partial cutting on moths.

2.3.6 Classification of moths into early- and late-season breeders

Moth species composition changes significantly between seasons (Work and McCullough 2000). Thus, the species comprising the lepidopteran assemblage might react differently to disturbance, depending on their developmental and phenological patterns. Based on life history knowledge and trap catch dates, moths were classified in two groups: early- and late-season breeders. Most of the early-season species (collected in May and June) overwintered as pupae, late-instar larvae or completed their development early in the spring. Similarly, most of the late-season species (collected from July to September) completed their larval development earlier in the summer that they were caught. This classification was based on moths collected during 1998 and 1999.

2.3.7 Classification of moths into host-plant range

Species were classified as mono-, oligo- or polyphagous species based on literature (Handfield *et al.* 1999; Miller and Hammond 2000). Monophagous species use one or several closely related host plants, usually in the same

genus. Good examples would be the beggar, *Eubaphe mendica* Walker, feeding exclusively on violets (*Viola* spp.) in northern Alberta or the gray scoopwing, *Callizia amorata* Packard, feeding on honeysuckle (*Lonicera* spp.). Oligophagous species feed on several host plants all belonging to the same family. The willow sphinx, *Smerinthus cerisyi* (Kirby), was placed in that category as it feeds on willows and poplars, which belong to the Salicaceae. Polyphagous species fed on and used plants from more than one family. The small engrailed, *Ectropis crepuscularia* (D.&S.) was the most polyphagous species classified, feeding on more than 70 species of plants (Handfield *et al.* 1999). This classification was also based on moths collected during 1998 and 1999.

2.3.8 Classification of moths into feeding guilds

Analysis of impact on feeding guilds is another way to investigate how harvesting influences the moth assemblage using a particular site. Species using the same resources are more likely to react in a similar way to disturbance. Indeed, Waring (1989) found that changes in availability of larval food plants were reflected in the moth community in his study. Species were classified based on current literature (Handfield *et al.* 1999; Miller and Hammond 2000) in ten feeding guilds: 1. Grass feeders, 2. Woody plant generalists, 3. Low and non-woody plant generalists, 4. Fungus and dead leaf feeders, 5. Salicaceae (poplars & willows) specialists, 6. Deciduous tree feeders, 7. Conifer feeders, 8. Lichen feeders, 9. Root feeders and 10.

Generalists. Moths captured over the entire three-year study (1998 to 2000) were classified into feeding guilds.

2.3.9 Analyses

Differences in moth species richness and total trap catches between forest types, treatments, years and by moth families were analysed using one- and two-way analyses of variance (ANOVA) with sampling nights as repeated measures (Zar 1996) in SPSS (1999) and SAS (1999). Because it is conservative and does not require equal sample size (Zar 1996), Scheffe's multiple comparison test was used to examine significant differences between means from ANOVA. A correlation analysis was performed to test if specific site characteristics (basal area, understory vegetation height and slope) affected the catches of 1999.

Non-metric multidimensional scaling (NMS) was chosen to analyse differences in species composition (see Work and McCullough 2000). It is often the method of choice for graphical representation of community relationships and has been used to associate species composition with disturbance effect in other studies (Clarke 1993). This iterative method ranks the data on a number of axes minimising 'stress' which is the departure from monotonicity between distance in the original matrix and distance in the ordination space. Clarke (1993) suggested the following rules of thumb based on practical experience for interpreting stress values: <5% stress gives an excellent representation with no prospect of misinterpretation, <10% stress represents a good ordination with no

real risk of drawing false inference, <20% stress can still lead to a usable picture but reliance should not be placed on the details of the plot and more than 20% stress is likely to yield plots that are dangerous to interpret. The Bray-Curtis coefficient of dissimilarity was used to measure distances in the original ordination space because it retains sensitivity in more heterogeneous data sets and gives less weight to outliers (McCune and Mefford 1999) compared to other distance measures.

Indicator species analysis (Dufrêne and Legendre 1997) was used to detect and describe the value of different lepidopteran species and feeding guilds for differentiating season, forest and treatment types. Indicator values ranging from 0 (no indication) to 100 (perfect indication) were calculated using species relative abundance and relative frequency. These values were tested for statistical significance using a Monte Carlo technique. The program PC-ORD version 4 (McCune and Mefford 1999) was used to conduct NMS [based on a program by Mather (1976) using Kruskal's algorithm (1964)] and indicator species analyses.

2.4 Results

2.4.1 Abundance and diversity

Overall, 293 species of moths were collected in light traps at EMEND. These included macrolepidopterans (higher Ditrysia: Superfamilies Geometroidea to Noctuoidea) and pest microlepidopterans (e.g. large aspen tortrix, *Choristoneura conflictana* Walker). Light traps yielded 12,856 moths on

213 trap-nights in 1998, 8927 moths on 196 trap-nights in 1999, and 7421 moths on 99 trap-nights in 2000. Total richness was 215 species in 1998, 242 species in 1999, and 187 species in 2000. There was an average 45% species overlap among the three years and the pattern of pairwise similarity (62% between 1998 and 1999, 54% between 1999 and 2000, and 47% between 1998 and 2000) suggesting that pre- and post-logging assemblages differ considerably. Geometridae and Noctuidae, the two largest families of macromoths, dominated the moth community in the number of genera and number of species (Table 2.1).

Species richness and moth trap catches were comparable among forest types investigated in both years (Tables 2.2 and 2.3). Species overlap ranged from 59 to 68% among three forest types, indicating a large group of shared species. Singletons, species with only one occurrence, totalled 31 in 1998, 40 in 1999, and 48 in 2000. No species with five specimens or more were found in only one forest type. However, the large majority of some species were found in certain forest types (see habitat use section below).

In 1999, both moth trap catch and species richness were significantly higher in control sites than in disturbed sites (Tables 2.3 and 2.10). However, unlike 20% RSC, species richness in 50% RSC did not differ significantly from that of control compartments. The lower species richness in the harvested compartments (Table 2.10) did not simply reflect low moth trap catch because the rarefaction curves were steeper in harvested compartments (Figure 2.2).

Indeed, equal sample sizes would be predicted to yield even more species in harvested sites compared to unharvested sites, but fewer specimens per species would be expected. There was no interaction between cover type and treatment with respect to effect on species richness (Table 2.3).

Even three years of trapping were not enough to capture the entire range of species present at EMEND sites as shown by the overall species accumulation curve (Figure 2.3). However, goals of this study mainly concentrated on the response of species to disturbance in relation to control sites; an exhaustive list of the lepidopteran fauna was thus not critical to meet our objectives. Furthermore, the main species have all been identified considering that the curves are beyond the inflection point of the species accumulation curve (Figure 2.3).

2.4.2 Environmental variables

Catch size appears to have been affected mainly by vegetation density at the trap level, given the suite of variables measured in this study. Basal area correlated positively with catch size ($R=0.552$, $p<0.01$) in 1999 after cutting. Also, the average height of understory vegetation was negatively correlated ($R=-0.632$, $p<0.01$) with catch size and independent of cover type (Table 2.4). Slope had no significant effect on catch size. The light interception by vegetation significantly increased between 5 and 20 meters away from the light trap (Figure 2.4), especially in control stands. This effect should have been expected to slightly increase trap catch in partially cut stands, especially in the

20% RSC, relative to uncut stands because light reaches farther in thinned stands and potentially attracts more moths. However, differences in trap catch expected to result from this effect were not detected.

2.4.3 Moth assemblage and habitat use

Based on trap catches over two years (1998 and 1999), 111 macro-moths species (43% of the total catch) were classified in a habitat use category. Of these, 64% were generalists, 20% were deciduous specialists and 16% were spruce specialists. The community was not clearly dominated by generalist species, perhaps partly due to the large numbers of unclassified moths. The community from undisturbed forest (1998) differed somewhat between deciduous dominated stands and stands with a coniferous component as shown on a two-dimensional NMS graph (Figure 2.5) where the two groups are separated. Conifer specialists such as *Xestia mixta* (Walker), *X. perquiritata* (Morris), *Feralia comstocki* Grote and *Panthea acronyctoides* (Walker), which were virtually absent in pure deciduous stands, were responsible for this forest type clustering. Certain species dependent on spruce or spruce-related resources (e.g. mosses, lichens) such as *Eilema bicolor* (Grote) and *Idia americalis* (Guenée), both lichen feeders on coniferous trees, were two to ten times more abundant in stands containing spruce than in pure deciduous stands.

Indicator species analysis identified 29 species associated with a specific forest type in 1998 (Table 2.5). In pure deciduous stands, eight of the indicator

species fed on deciduous trees, four were low and woody plants feeders, two were generalist feeders, one fed on roots, possibly grass (Graminae) roots and one species had unknown food plants. Eight species were indicators of deciduous stands with a spruce understory: three were generalist feeders, two fed on low and woody plants, one fed on deciduous trees and two were unknowns. Finally, in coniferous stands, indicator species fed on spruce (1 sp.), conifer lichens (1 sp.), willows (1 sp.) or had unknown food plants (2 spp.).

Moths are generally grouped into families based on their structural similarity. Noctuid moths, for example, are generally robust-bodied, strong fliers, thus more likely to have greater mobility than most geometrid moths. In contrast, geometrid moths have a higher wing to body size ratio and slower, less efficient flight. Less mobile moths are presumably less likely to venture outside their natural environment (e.g. forests, marshes, grass fields). After disturbance, the relative percentage of noctuids caught in all stand types increased from 29% to 38% in 1999 and 40% in 2000. Conversely, the overall relative percentage of geometrids fell from 52% in 1998 down to 31% and 21% in 1999 and 2000 respectively. However, between-year comparisons of light trap samples are often subject to large fluctuations in numbers (Rejmánek and Spitzer 1982; Kobro 1991) and composition (Butler and Kondo 1991; Sample *et al.* 1996). Thus, we must investigate differences between treatments year by year to factor out annual fluctuations. Significant decreases in trap catch in logged compartments appeared in three lepidopteran families: Noctuidae

($p<<0.001$), Geometridae ($p<0.001$), and Uraniidae ($p=0.003$) (Tables 2.6 and 2.7). Negative changes were also found in species richness of the Geometridae ($p<<0.001$) and Notodontidae ($p=0.038$) (Tables 2.8 and 2.9).

Two noctuid species were positively affected by disturbance: *Protolampra rufipectus* (Morr.) and *Platyperigea montana* (Bremer). From 1998 to 2000, numbers caught went from one to 51 and 104 for *P. rufipectus* and from zero to 35 and 28 for *P. montana*. These species were mainly caught (75 to 90% of captures) in logged compartments.

There were significantly more species in control sites than in sites subjected to partial cutting treatments (Table 2.10). Moreover, trap catch of generalists did not increase with thinning intensity as predicted, but decreased slightly (Table 2.11). Data on number of individuals did show a higher proportion of spruce specialists in the 20% RSC than in the other compartments. This increase was driven by three noctuid species: *Xylena thoracica* (Putnam-Cramer), *Nycteola frigidana* (Walker), and *Platyperigea montana* (Bremer).

The moth assemblage was affected by disturbance (Figure 2.6). The left-to-right separation of the disturbance gradient (axis 1) explained most of the variation ($R^2=0.71$) in rank similarities between sites. Moth assemblages in control sites clustered tightly together in comparison to those in the disturbed sites plotted in the ordination space. The 50% RSC were almost all located between the two other treatments, leaving 20% RSC farther away from the

control and more dispersed in the ordination space than the trap catches from the other sites. Moth assemblages were thus least similar between the control compartments and those subjected to the highest level of disturbance.

2.4.4 Early- and late-season breeders

The moth community differed considerably between early- and late-season species (Figure 2.7). Only well represented early- and late-season species were chosen to investigate partial cutting impacts. Therefore, 45 and 72 adult species were chosen as species indicators of early and late season, respectively. On the NMS two-dimensional graph (Figure 2.8), axis 1 explained the difference in moth assemblage between seasons. It also showed striking variation in moth assemblages between 1998 and 1999. Axis 2 represented cutting impacts on the moth community. Mean trap catches were calculated over all sites for early- and late-season indicator species (Figure 2.9). Differences in trap catch between early- and late-season species resulted from the number of species classified in each category (45 and 72 species, respectively). There was a decrease in moth numbers in both groups as disturbance increased.

2.4.5 Host-plant range

Proportions of 261 moths classified into the three host-plant range groups were similar between 1998 and 1999 based on number of species (Table 2.12). About half the community was dominated by polyphagous species. However, the trap catch of monophagous species in harvested stands

decreased by half following partial cutting (Table 2.13). Trap catch of oligophagous species slightly increased with the amount of disturbance. This last trend was driven by species having salicaceous plants as their main hosts. Sixty percent of the moths caught in 20% RSC were in that category.

2.4.6 Feeding guilds

Control sites had proportionally more species of the guilds feeding on woody plants, deciduous trees, conifers and lichens than partially cut sites two years post-harvest (Figure 2.10). However, lepidopterans using grass, Salicaceae and a wide range of plants as larval hosts were more numerous in disturbed sites than in controls. Proportions of species in other guilds were not affected significantly. We also used indicator species to evaluate whether feeding guilds were related to forest harvesting impact. One year following partial cutting, indicators of disturbance were found in four feeding guilds: low and woody plants generalists, conifers and deciduous trees specialists (Table 2.14). Two years following harvest, indicators were found in six feeding guilds (Table 2.15), with the addition of the Salicaceae specialists and lichens feeders to the four feeding guilds identified on these sites in 1999.

2.5 Discussion

2.5.1 Abundance and diversity

There were no striking differences in moth trap catch and richness among the three cover types investigated. As hypothesized, each forest type

shared many common species and no species with more than four specimens was found solely in one forest type. The relative homogeneity of understory vegetation composition across cover types (EMEND core study 1998, unpublished data) might explain this large proportion of shared species. Indeed, in our study, at least 35% of the species found relied on understory plants as caterpillars, another 50% of the species had at least some of their host plants in the understory, and adults of many species fed on nectar from flowering plants. Moreover the generally slow response of vegetation one year after disturbance (Dyrness 1973) was observed at EMEND and this might explain the lack of difference between 1998 and 1999 moth data. Species overlap between years (including year 2000) suggested that moth assemblages grew further apart with time, possibly influenced by response of vegetation to harvest.

Partial cutting had an adverse effect on both moth species richness and overall trap catch. Trap catch was particularly influenced by forest harvesting as both treatments (20 and 50% residual structure) had significantly lower moth counts than controls (90% and 83% decrease, respectively). However, moth species richness was significantly lower only in 20% RSC, compared to uncut sites, with a 33% decrease. Thus it appears that recent logging reduces the number of moths flying in a stand more than it affects number of species.

Usher and Keiller (1998) showed that the most important factor determining woodland moth species richness was the plant species richness. If

reductions in moth species number observed at EMEND are primarily a function of loss or reduction in abundance of plant species, there is high probability of full recovery to pre-harvest species composition over time, given refuges nearby to sustain populations of potential colonists. Over the long run in harvested stands, plant species richness will return to pre-disturbance levels (Halpern and Spies 1995), and in fact, plant richness might even be higher following partial cutting due to a higher vertical and horizontal spatial heterogeneity (Shafi and Yarranton 1973). This diversification of the plant community may well attract even more moth species during the mid-successional phases.

Species richness and catch per trap-night were highly correlated in our study (R^2=0.89, $p<0.01$) as also shown by Daily and Ehrlich (1996) at sites in Costa Rica. However, lower species richness in disturbed sites at EMEND was not a sampling artifact caused by lower moth abundance. Indeed rarefaction curves show a faster accumulation of moth species in 20% and 50% RSC for the same sample size. Thus, it seems certain that extensive low-retention logging over a wide area will threaten local populations of some night flying moths. Work on dispersal capacity of boreal moths is required to address this uncertainty. Data from EMEND do, however, suggest that boreal moths characteristic of deep forest are reluctant to cross recent clearcuts (Morneau, unpublished data) and thus landscape considerations could well be important.

2.5.2 Environmental conditions

Thinning affected the moth community mainly by changing local conditions in the first year post-harvesting. In general, logging reduces the amount of canopy cover (reflected in the basal area), increases air circulation (affecting temperature and wind), precipitation reaching the forest floor and solar radiation penetrating the stand (Safranyik *et al.* 1998). Environmental conditions thus created were obviously harsher for moths of the forest interior. A partially cut, open stand is more subject to larger fluctuations in microclimate than a stand with an intact canopy acting as a buffer for understory microclimate. This change in conditions probably resulted in a lower number of moths caught in logged stands at EMEND although, given present data, the cause is elusive. Changes in microclimate could increase emigration rate, decrease immigration rate (along with changes to surrounding conditions) or decrease larval survivorship.

In addition to microclimatic effects, higher and denser understory vegetation potentially reduced the efficiency of the light trap by intercepting light transmission therefore resulting in a potentially lower number of specimens caught in control sites. The light interception by vegetation increased dramatically with distance from trap, especially in the unharvested stands. Because understory vegetation height was independent of cover type, data about moth assemblages were not biased by this factor at the stand level. Light interception probably played a lesser role on trap catch among treatments than

other factors such as temperature or wind. Indeed, trap catches were higher in uncut stands even with a greater light interception compared to partially cut stands. Thus, negative treatment effect on trap catch could have been even more significant without light interception by vegetation, more so in 20% RSC than in 50% RSC compared to controls.

Lower trap catch of moths in partially cut stands could also be due to lower local recruitment. Less foliage following thinning might result in a lower number of caterpillars as suggested by Liebhold *et al.* (1998). However, it is impossible to quantify this effect on light trap catches as, to our knowledge, no study has investigated the proportion of local moths versus dispersing moths coming from another stand type in a continuous forest.

Thinning might also modify other factors affecting lepidopteran populations such as predation, parasitism and disease. However, Grusheky *et al.* (1998) could demonstrate no significant effect of thinning on predation of larvae and pupae of a polyphagous species, the gypsy moth, by small mammal predators (although the population of the latter was increased). Similarly, Liebhold *et al.* (1998) reported no observable effect of thinning on rates of parasitism or disease in gypsy moth populations. Unfortunately, this polyphagous outbreak species is atypical of lepidopterans in the present study because it is an exotic species, not carrying its entire suite of co-evolved natural ennemies and diseases (Ferguson 1978). Studies of predation, parasitism and disease are thus needed on other species in thinned and unthinned stands to

better understand factors leading to the observed decline in lepidopteran numbers.

2.5.3 Habitat use

The moth community was dominated in numbers by habitat use generalist species. The pre-disturbance community was more similar between the two cover types with a spruce component (under- and overstory) than deciduous stands. Differences in moth assemblages were caused by the presence of conifer specialists and species dependent on spruce-related (Roberts 1996) and other resources such as overmature trees (Greatorex-Davies and Marrs 1989). A similar effect was also demonstrated in a comparative light trapping study by Waring (1989). Based on indicator species, control sites from each forest type were characterized by moths with different feeding preferences. Deciduous stands were mostly characterized by species with larvae feeding on overstory trees and understory plants. Mixed stands were characterized by generalist feeders and understory specialists. Finally, species tightly associated with humid spruce stand plants (spruce and conifer lichen feeders, willow feeders) were indicators of coniferous stands.

Judging from their general body features, certain groups of moths should be more mobile than others (Scoble 1992; Nieminen *et al.* 1999). This sort of variation in flight ability may influence moth resilience to changing environmental conditions. For example, trap catch of larger moths that are generally highly mobile such as hawkmoths (Scoble 1992), family Sphingidae,

was not affected by thinning, although small moths like the only Uraniidae species caught, *Callizia amorata* Packard, seemed to be strongly affected. In 1999, between-site differences across treatments clearly showed a differential effect of environmental conditions on certain moth families. Partial cutting negatively affected trap catch of Noctuidae, Geometridae, Uraniidae and species richness of Geometridae and Notodontidae. Significant changes in the last two families occurred only between control compartments and 20% RSC. All other negative impacts were significant between control and both levels of cutting. Between-year differences seemed to indicate a decrease in overall geometrid trap catch following disturbance compared to sphingids, represented by two *Smerinthus* species (non-functional mouthparts, strong fliers) accounting for 99.9% of the hawkmoths trapped, and noctuids, which are robust-bodied, hence thought to be strong fliers. These results support Scoble's 1992 view on the value of Geometridae as indicators of environmental quality due to their relatively restricted mobility compared to other moth families. Thus, moth body size and related flight capability may have influenced the habitat use by different moth families.

There was only slight evidence of the hypothesized increase in habitat generalist species following cutting treatments. The plant community probably did not change enough in the year following winter harvesting to drive a change in moth species composition. In a study by Halpern and Spies (1995), understory plant richness decreased by 24-29% after one growing season post-

logging although losses in plant species diversity were short-lived and plant species richness exceeded pre-harvest levels within one to three years. In another study by Peterson and Pickett (1995), it similarly took two growing seasons after an old-growth forest blowdown to result in an increase in plant richness. Also, invading plant species were not found until two years after logging in old-growth Pacific forests (Dyrness 1973). Finally, Thomas *et al.* (1999) demonstrated that twelve to sixteen years after thinning, understory plant cover and richness were higher, especially for the herb and shrub layers. In our study, delayed disturbance effects on the understory plant community was probably reflected in the data about moth assemblages, as changes in species richness for different feeding guilds over two years following treatment (discussed in feeding guilds section).

Some species of moths might be adapted for ephemeral habitats and thus able to respond rapidly to change (Woiwod and Stewart 1990). Moths caught in harvested and control compartments were thus compared. Late-season noctuids *Protolampra rufipectus* (Morr.) and *Platyperigea montana* (Bremer) were caught mainly in disturbed habitats. On average, however, there was little evidence that many species took advantage of newly created conditions following disturbance. Instead, some species were relatively more abundant than others because of resilience to environmental changes following disturbance. The post-disturbance NMS analysis clearly shows disturbance impact on moths based on species composition: control sites cluster tightly

together, reflecting a more similar moth community than in disturbed sites. The increased number of spruce specialist species in highly disturbed sites with only 20% residual structure was driven by three noctuid species. An association with open woodlands might explain an increase in abundance of *Xylena thoracica* (Putnam-Cramer). Other factors, not measured here, such as changes in parasitoid populations may explain these changes for *Platyperigea montana* (Bremer) and *Nycteola frigidana* (Walker) as parasitoids are a main causative factor of variations in lepidopteran populations (Berryman 1996).

2.5.4 Early- versus late-flyers

Thinning might also have affected moth species in the first post-harvest year by destroying or removing eggs, pupae and overwintering larvae *per se*. Species assemblages differed between cut and uncut sites, although this variation was swamped by that documented between seasons and years. Were late-season species spending their first winter following disturbance as exposed eggs or as young larvae more negatively affected than early-season ones as hypothesised? Trap catch data showed no difference on average between those two groups. Numbers of both groups decreased similarly as thinning intensity increased. Juvenile survivorship subsequent to harvest for late-season species overwintering as eggs or young larvae might have been affected negatively in the year following disturbance by thinning compared to early-season species but it was not detected in this study. Late-season indicators were less numerous in 1998 than in 1999 based on data from control

sites. This change was driven mainly by one species, *Choristoneura conflictana* Walker, this species was in outbreak during 1999 with over 2000 individuals captured in light traps. In 1998, more early-season species were caught compared to late-season ones due to large abundance of two geometrids, *Ectropis crepuscularia* (D.&S.) and *Venusia pearsalii* (Dyer) and one hawkmoth, *Smerinthus cerisyi* Kirby. No difference could be demonstrated in the overall data between early- or late-season moths, perhaps due to large species-dependent yearly fluctuations. However, lower numbers of moths caught in thinned compartments compared to control compartments confirmed a disturbance impact.

2.5.5 Host-plant range

The moth community at EMEND appears to be organized to exploit a broad defoliator niche by using diverse host-plant range and feeding strategies. Host-plant range proportions for noctuid species at EMEND were similar to those observed in a British study (Inkinen 1994). In general, monophagous species were less abundant than oligo- and polyphagous species. This is expected since larger moths tend to be more polyphagous (Niemelä *et al.* 1981, Gaston and Reavey 1989, Loder *et al.* 1998) and better dispersers. Thus, polyphagous species would travel more through recently disturbed habitats than monophagous species. In addition, monophagous species are known to migrate less (Nieminen *et al.* 1999) and are also believed to be more sensitive to disturbance. Kitahara and Fujii (1994) showed, for example, that species

richness of specialist feeding butterflies (i.e. monophagous species) decreased when human disturbance increased. In their study, specialists were less abundant than generalists (i.e. polyphagous species), which is also consistent with the results from moths at EMEND.

Oligophagous species were slightly more abundant in disturbed sites than in control sites. Changes in the availability of larval food plants following harvesting can have an impact on moth assemblages (Waring 1989). For example, one-year old aspen suckers following harvesting most probably drew oligophagous moth species to those sites as larvae of many of these species feed on salicaceous plants and female adults are attracted to them to lay their eggs.

Lack of a large difference between host-plant proportions after disturbance probably reflects a delay in moth response to disturbance. Indeed, many moths flying in 1999 were already pupating when the partial cutting occurred in the winter of the preceding year. Thus larvae were not exposed to thinned stand conditions and changes in environmental conditions would not be fully reflected on the moth community before summer 2000, two years after the cut.

2.5.6 Feeding guilds

Feeding guilds can be used to examine indirectly disturbance impact on plants using two years of post-disturbance data. An increase in the number of generalist moth species was caused by the suggested short-term increase in

plant species richness following harvesting. The greater number of host plants present attracted more moth species. Also, an increase in moth species richness found in disturbed sites for species feeding on grass and salicaceous plants was caused by the invasion of the stands by grasses and pioneer trees such as trembling aspen and balsam poplar. Disturbance reduced cover of both deciduous and coniferous trees, woody plants and lichens on trees which explained why moth species associated with these feeding guilds were found in lower proportions on partially cut stands. Indicator species analysis based on feeding guilds gave similar results. Indeed, one year following partial cutting, indicators of disturbance were found in four feeding guilds: low and woody plants generalists, conifers and deciduous trees specialists (Table 2.14). Two years following harvest, indicators were found as two additional feeding guilds (Table 2.15): specialists on Salicaceae and lichen feeders. Disturbance, thus, had a tangible but indirect impact on the moth community by modifying feeding resources.

2.6 Conclusion

Moth species richness and trap catch before disturbance were similar among the three forest types investigated. Moth species assemblages were also quite similar between forest types although stands with a spruce component were more similar due to the presence of a few spruce specialist

species. The moth community of this mixed boreal forest had a large share of habitat generalist species.

One year following partial cutting, moth species richness and particularly moth trap catch were negatively affected by changed environmental conditions in residual stands and by the removal *per se* of eggs, pupae and overwintering larvae by harvest treatments. Early- and late-season moth species reacted in the same way to thinning. The moth community differed more between sites as the degree of disturbance increased. Moth families were also differentially affected by disturbance. Small-bodied moths such as loopers (family Geometridae) were affected more negatively than others, probably because of the generally positive relationship between body size and dispersal ability. Few moth species displayed a positive response in the summer after winter logging, perhaps because the plant community had not had a growing season yet to react to disturbance. However, data collected two years after cut showed that moths, once grouped by feeding guilds, had a differential response to partial cutting. Species feeding on early successional plants or having a broad selection of host plants were more diverse in disturbed sites compared to uncut sites. The opposite was also true for species feeding on shrubs, and on deciduous and coniferous trees.

The moth community should return to its pre-disturbance conditions with time assuming that enough unharvested stands are left on the landscape for disturbance-sensitive moths to disperse from. Partial cutting showed that many

moth species would still be using disturbed habitat in a significant way, possibly due to their good dispersal abilities through a patchy landscape. Partial cutting might even prove to be an alternative to clearcutting that is more friendly to biodiversity. In the long run, partial cutting at different scales might even increase moth species diversity by increasing spatial heterogeneity and consequently plant diversity, an important determinant of moth species richness. Continued study of the EMEND moth community over the next few years would provide more complete answers on how moths respond to plant succession. Other factors like parasitism, predation, and occurrence of disease should also be studied following partial cutting, as they may be major actors affecting the moth community.

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Table 2.1 Total number of macromoth individuals, species and genera captured by light trapping at all study locations on the EMEND site from 1998 to 2000.

Family	Individuals	Genera	Species
Geometridae	9231	61	88
Noctuidae	8039	92	153
Sphingidae	2259	3	4
Notodontidae	1002	6	11
Lasiocampidae	626	11	14
Uraniidae	577	1	1
Arctiidae	541	2	2
Drepanidae	185	5	6
Hepialidae	49	2	2
Lymantriidae	40	1	1
Saturniidae	7	1	1

Table 2.2 ANOVA table of moth species richness and trap catch between cover types in undisturbed forest (1998).

Source of variation	d.f.	MS	F	P
Moth richness				
Cover type	2	79.8	1.32	0.32
Error	9	60.5		
Moth trap catch				
Cover type	2	2813.8	0.60	0.57
Error	9	4685.6		

Table 2.3 ANOVA table of moth species richness and trap catch between cover types and treatments in 1999.

Source of variation	d.f.	MS	F	P
Moth richness				
Cover type	2	28.3	0.27	0.78
Treatment	2	1457.6	13.71	0.03*
Cover*Treat	4	59.3	0.56	0.71
Error	3	106.3		
Moth trap catch				
Cover type	2	1121.5	0.28	0.78
Treatment	2	50872.0	12.53	0.04*
Cover*Treat	4	1635.2	0.40	0.80
Error	3	4059.1		

Table 2.4 Average shrub height by cover type (1998) (N=2211).

Cover type	Height (m ± SD)
Deciduous	2.26 ± 0.93
Mixed	2.17 ± 1.34
Coniferous	2.36 ± 1.31

Table 2.5 Indicator species of differences in moth assemblage between deciduous, mixed and coniferous stands (1998).

Family	Species	Stand	Observed indicator value	Indicator values from randomized tests	
				Mean ± SD	P
Noctuidae	*Anathix puta* (G. & R.)	Deciduous	81.2	28.5 ± 9.9	0.001
Noctuidae	*Oligia illocata* (Wlk.)	Deciduous	77.6	29.8 ± 9.5	0.001
Noctuidae	*Orthosia revicta* (Morr.)	Deciduous	70.0	37.7 ± 7.6	0.001
Geometridae	*Semiothisa ulsterata* (Pears.)	Deciduous	72.1	30.7 ± 8.7	0.001
Geometridae	*Iridopsis larvaria* (Gn.)	Deciduous	70.6	32.8 ± 8.6	0.002
Arctiidae	*Lophocampa maculata* Harr.	Deciduous	68.7	23.4 ± 9.7	0.002
Noctuidae	*Orthosia hibisci* (Gn.)	Deciduous	68.4	27.9 ± 9.4	0.002
Geometridae	*Ennomos magnaria* Gn.	Deciduous	72.7	36.9 ± 12.1	0.005
Noctuidae	*Oligia mactata* (Gn.)	Deciduous	65.2	36.0 ± 8.4	0.005
Geometridae	*Orthofidonia exornata* (Wlk.)	Deciduous	61.5	38.3 ± 7.1	0.005
Noctuidae	*Brachylomia discinigra* (Wlk.)	Deciduous	66.7	31.7 ± 10.0	0.008
Noctuidae	*Orthosia segregata* (Sm.)	Deciduous	60.8	32.4 ± 8.2	0.009
Noctuidae	*Platypolia anceps* (Steph.)	Deciduous	54.5	37.3 ± 6.5	0.014
Noctuidae	*Palthis angulalis* (Hbn.)	Deciduous	50.0	17.7 ± 8.2	0.020
Geometridae	*Protitame virginalis* (Hulst)	Deciduous	57.4	37.4 ± 9.8	0.050
Noctuidae	*Lithomoia germana* (Morr.)	Mixed	62.5	19.0 ± 8.4	0.003
Noctuidae	*Xestia mixta* (Wlk.)	Mixed	57.1	34.7 ± 7.6	0.007
Geometridae	*Scopula* spp.	Mixed	52.8	40.5 ± 4.8	0.009
Noctuidae	*Xylotype acadia* B. & Benj.	Mixed	61.5	36.3 ± 8.3	0.013
Noctuidae	*Diarsia dislocata* (Sm.)	Mixed	57.3	34.1 ± 8.5	0.014
Noctuidae	*Polia nimbosa* (Gn.)	Mixed	62.2	35.7 ± 8.6	0.018
Geometridae	*Epirrita autumnata* (Bkh.)	Mixed	56.1	38.1 ± 7.1	0.022
Geometridae	*Eustroma semiatrata* (Hulst)	Mixed	59.1	40.0 ± 8.1	0.028
Hepialidae	*Gazoryctra hyperborea* Mösch.	Mixed	51.9	31.5 ± 8.9	0.041
Geometridae	*Operophtera bruceata* (Hulst)	Coniferous	63.9	31.1 ± 9.8	0.014
Tortricidae	*Petrova burkeana* Kft.	Coniferous	43.7	21.7 ± 9.3	0.025
Arctiidae	*Eilema bicolor* (Grt.)	Coniferous	50.0	27.0 ± 9.0	0.041
Tortricidae	*Choristoneura fumiferana* (Morr.)	Coniferous	48.3	28.8 ± 10.3	0.045
Noctuidae	*Polychrysia esmeralda* (Oberth.)	Coniferous	48.6	30.5 ± 9.2	0.048

Table 2.6 ANOVA table of treatment impact on number of individuals caught in light traps by family (N=12).

Source of variation	d.f.	MS	F	P
Noctuidae				
Treatment	2	46232.17	24.33	<0.001*
Error	9	1899.93		
Geometridae				
Treatment	2	49760.33	15.65	<0.001*
Error	9	3179.26		
Notodontidae				
Treatment	2	40.13	1.41	0.293
Error	9	28.44		
Sphingidae				
Treatment	2	85.13	3.11	0.094
Error	9	27.41		
Lasiocampidae				
Treatment	2	1339.13	2.14	0.174
Error	9	626.30		
Arctiidae				
Treatment	2	16.50	0.69	0.525
Error	9	23.86		
Drepanidae				
Treatment	2	18.00	1.06	0.386
Error	9	16.96		
Uraniidae				
Treatment	2	155.79	12.16	0.003*
Error	9	12.82		

Table 2.7 Treatment effect on number of individuals caught in light traps by family in 1999. Numbers with the same letter indicate no significant difference based on Scheffé's multiple comparisons test ($p<0.05$) (N=12).

Treatment	Noctuidae	Geometridae	Uraniidae
CONTROL	266.7 [b]	227.0 [b]	11.0 [b]
50% RESIDUAL	121.0 [a]	66.7 [a]	1.33 [a]
20% RESIDUAL	69.0 [a]	27.3 [a]	0.33 [a]

Table 2.8 ANOVA table of treatment impact on moth species richness by family (N=12).

Source of variation	d.f.	MS	F	P
Noctuidae				
Treatment	2	116.13	2.04	0.186
Error	9	56.96		
Geometridae				
Treatment	2	572.38	14.80	0.001*
Error	9	38.69		
Notodontidae				
Treatment	2	8.17	4.79	0.038*
Error	9	1.70		
Sphingidae				
Treatment	2	0.38	0.81	0.475
Error	9	0.46		
Lasiocampidae				
Treatment	2	1.83	4.13	0.054
Error	9	0.44		
Arctiidae				
Treatment	2	2.83	2.13	0.175
Error	9	1.50		
Drepanidae				
Treatment	2	2.75	1.83	0.215
Error	9	1.33		
Uraniidae				
Treatment	2	0.46	3.09	0.095
Error	9	0.15		

Table 2.9 Treatment effect on 1999 moth richness by family. Numbers with the same letters indicate no significant difference based on Scheffé's multiple comparisons test ($p<0.05$) (N=12).

Treatment	Geometridae	Notodontidae
CONTROL	36.8 [a]	3.3 [a]
50% RESIDUAL	21.7 [a]	1.0 [a]
20% RESIDUAL	14.3 [a]	1.0 [a]

Table 2.10 Total number of species and individuals trapped by forest type and treatments during 1999. Numbers with the same letters indicate no significant difference based on Scheffé's multiple comparisons test ($p<0.05$) (N=12).

Forest type / treatment	Richness Mean ± SE	Trap catch Mean ± SE
Deciduous	83.3 ± 17.4 [a]	56.1 ± 15.9 [a]
Mixed	89.0 ± 4.9 [a]	42.1 ± 9.9 [a]
Coniferous	83.3 ± 12.3 [a]	36.0 ± 9.5 [a]
CONTROL	101.7 ± 5.9 [b]	74.0 ± 13.9 [b]
50% RESIDUAL	76.0 ± 9.1 [a,b]	20.1 ± 4.8 [a]
20% RESIDUAL	61.3 ± 10.5 [a]	10.8 ± 2.6 [a]

Table 2.11 Number of moths caught in 1999 in each habitat use class by treatment.

Moth habitat use classes	CONTROL	50% RSC	20% RSC
Generalist	60.0%	58.5%	52.9%
Deciduous specialist	21.8%	13.1%	12.1%
Coniferous specialist	6.4%	6.2%	14.2%
Unknown	11.8%	22.2%	20.9%
Total	100.0%	100.0%	100.0%

Table 2.12 Number of moth species by host-plant range and year.

Host-plant range	1998	1999	Total
Polyphagous	104 spp.	119 spp.	156 spp.
Oligophagous	48 spp.	55 spp.	66 spp.
Monophagous	28 spp.	29 spp.	38 spp.

Table 2.13 Host-plant range proportions of moth species between treatments by species richness and abundance (1999).

Richness	CONTROL	50% RSC	20% RSC
Polyphagous	58.0%	59.3%	65.2%
Oligophagous	26.6%	27.9%	21.7%
Monophagous	15.4%	12.8%	13.0%
Abundance	**CONTROL**	**50% RSC**	**20% RSC**
Polyphagous	63.3%	65.0%	60.7%
Oligophagous	22.1%	27.1%	31.3%
Monophagous	14.6%	7.9%	8.0%

Table 2.14 Indicators of differences in species between partially cut and uncut compartments following logging (1999) based on feeding preferences.

Feeding guild	No. species in guild	Observed indicator value	Indicator values from randomized tests	
			Mean ± SD	P
Low plants generalist	29	74.8	55.5 ± 6.17	0.006*
Woody plants generalist	24	73.3	55.3 ± 6.16	0.009*
Conifers specialist	17	73.0	55.0 ± 7.80	0.024*
Deciduous trees specialist	51	68.0	56.3 ± 6.08	0.036*
Generalists	28	64.9	55.6 ± 5.77	0.072
Salicaceae specialist	37	73.0	62.2 ± 7.70	0.087
Fungus/dead leaves feeder	4	54.4	41.5 ± 8.38	0.098
Roots feeder	2	16.7	17.1 ± 7.28	0.475
Lichens feeder	2	46.9	50.0 ± 6.90	0.624
Grass feeder	10	49.9	53.1 ± 5.65	0.678

Table 2.15 Indicators of differences in species between partially cut and uncut compartments 2 years after logging (2000) based on feeding preferences.

Feeding guild	No. species in guild	Observed indicator value	Indicator values from randomized tests	
			Mean ± SD	P
Deciduous trees specialist	32	80.8	63.2 ± 6.59	0.002*
Woody plants generalist	17	85.1	57.2 ± 8.61	0.004*
Salicaceae specialist	27	92.2	67.8 ± 11.61	0.004*
Low plants generalist	26	80.5	57.2 ± 8.52	0.009*
Conifers specialist	14	88.1	52.7 ± 12.11	0.013*
Lichens feeder	3	89.1	51.6 ± 14.3	0.021*
Generalists	27	65.3	57.5 ± 5.14	0.092
Grass feeder	6	47.6	58.1 ± 8.84	0.878
Roots feeder	3	28.6	36.0 ± 12.06	0.926
Fungus/dead leaves feeder	2	16.7	16.7 ± 0.17	1.000

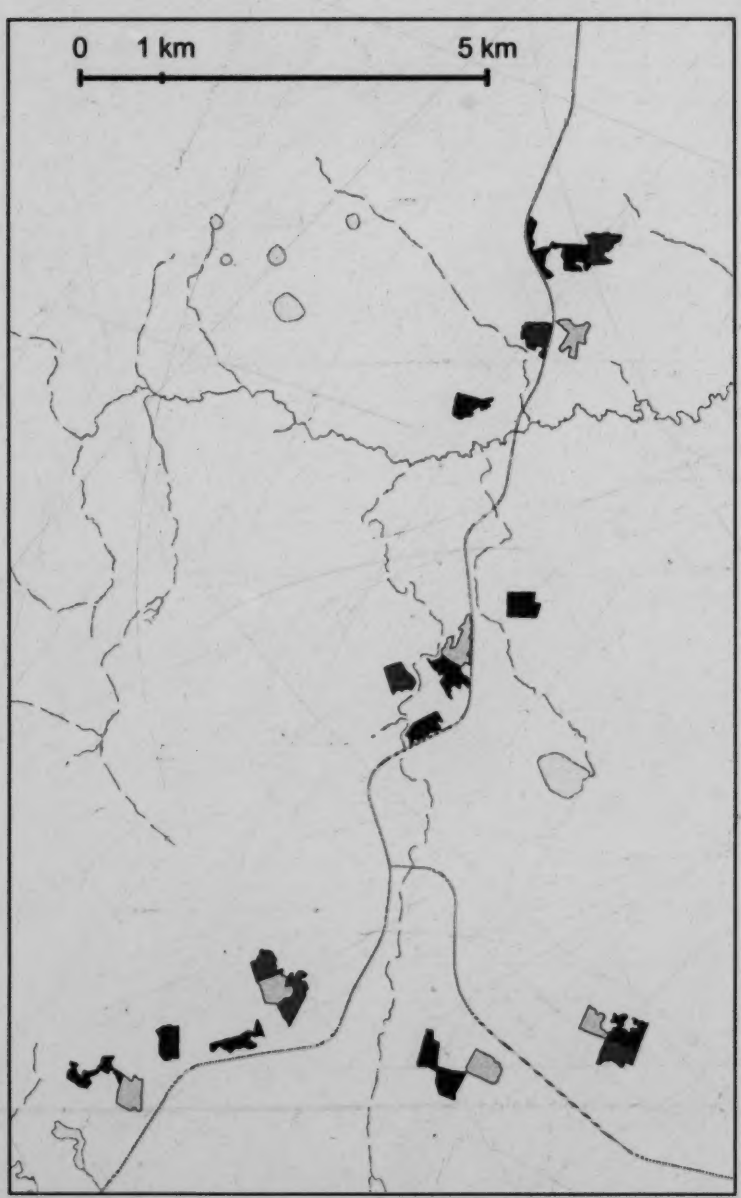

Figure 2.1 EMEND map showing compartments (control in black, 50% residual in dark grey and 20% residual in light grey) used in the study, roads and streams.

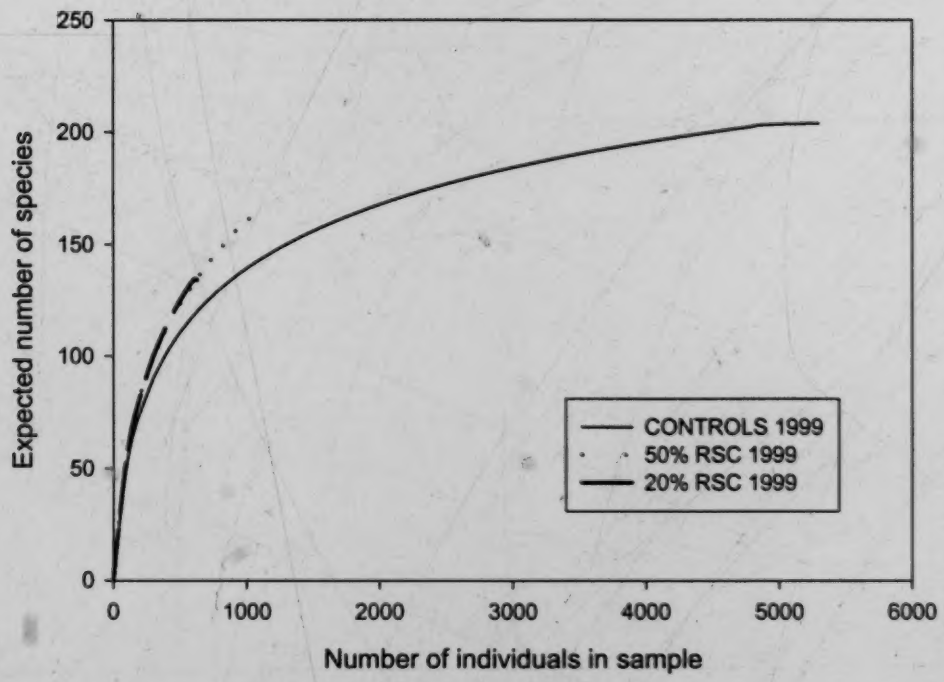

Figure 2.2 Rarefaction curves of the macromoth community in three different treatments (1999) (N=24).

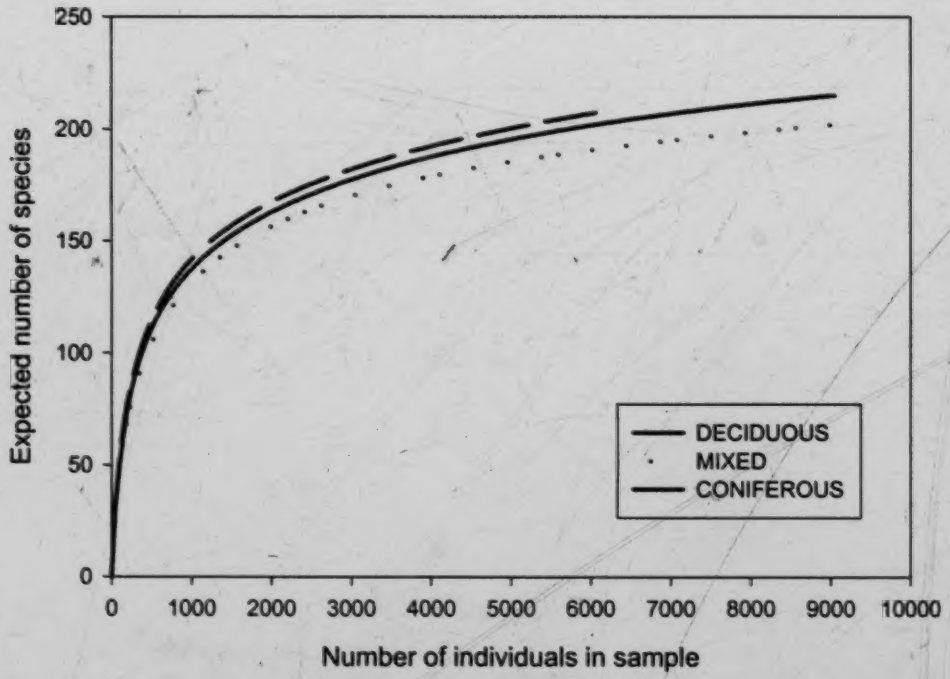

Figure 2.3 Rarefaction curves of the macromoth community in three forest types (1998-2000).

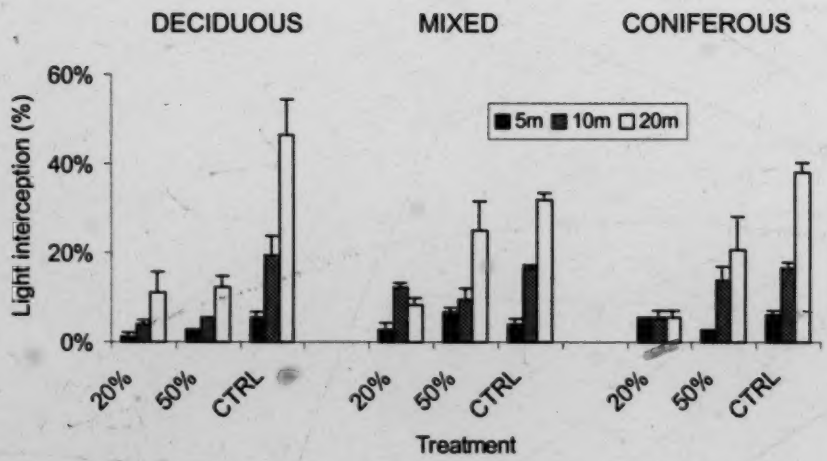

Figure 2.4 Vegetation interference to light (±SE) by cover type and treatment (1999).

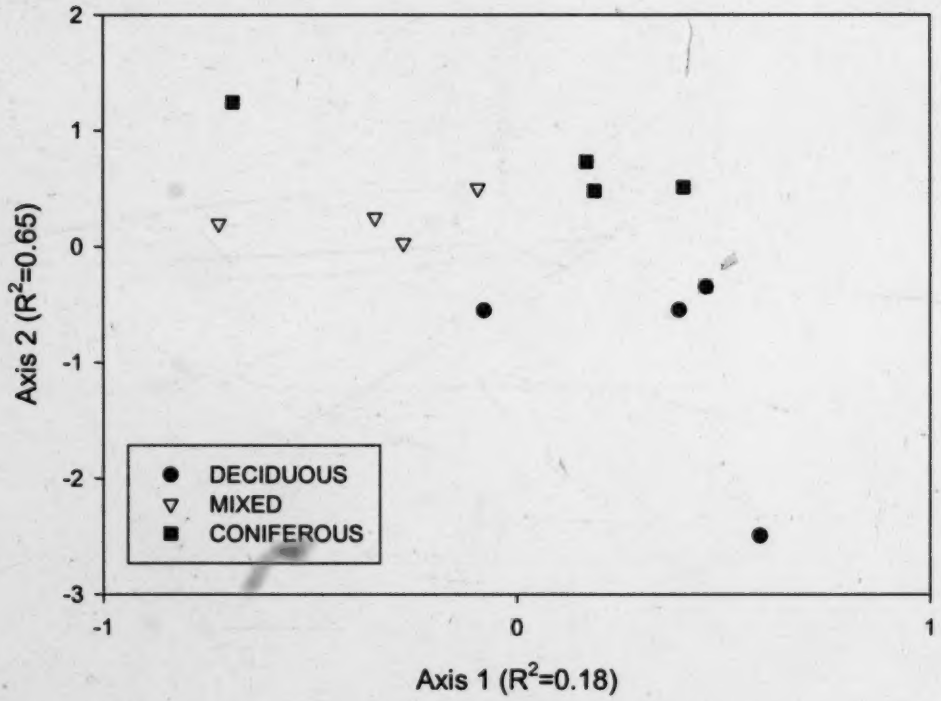

Figure 2.5 Two-dimensional NMS solution of the pre-disturbance moth community (1998) by forest type (R^2_{tot}=0.83, stress=11.1%, p=0.03) (N=12).

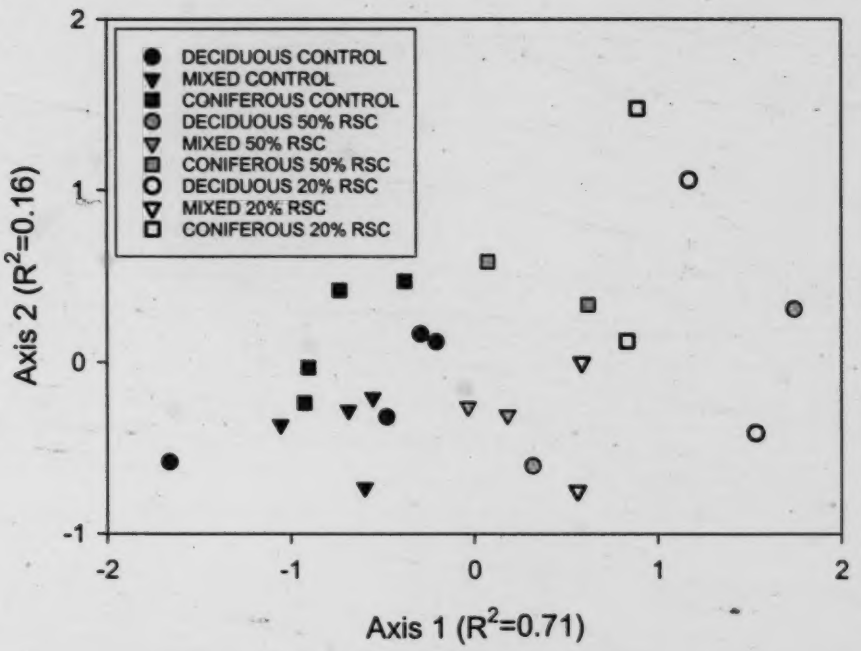

Figure 2.6 Two-dimensional NMS solution of the post-disturbance moth community (1999) by forest type and treatment (R^2_{tot}=0.87, stress=10.5%, p=0.03) (N=24).

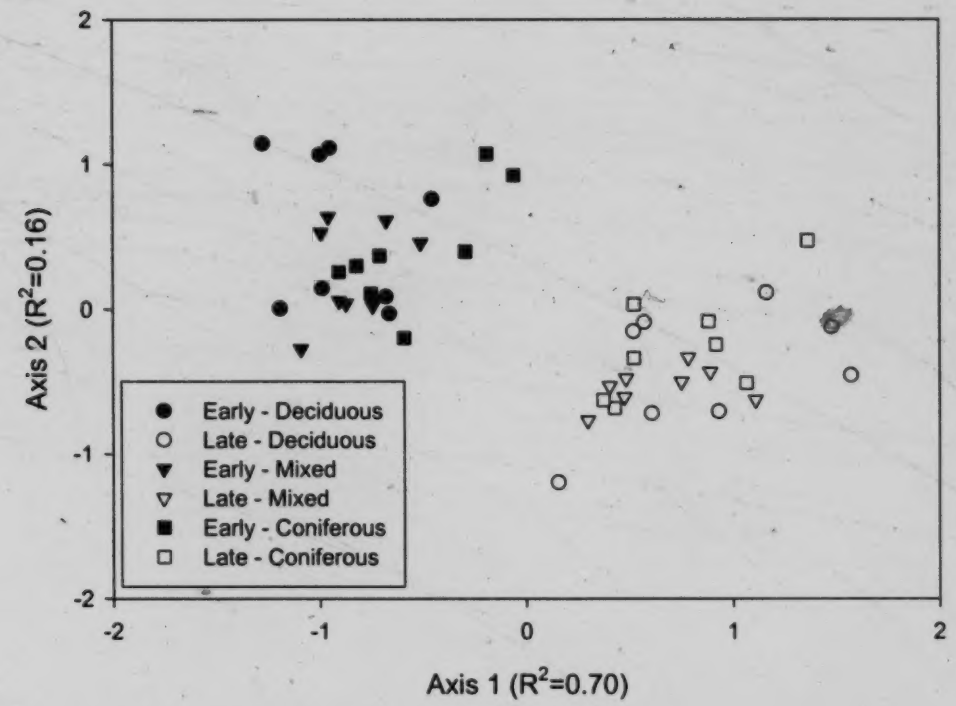

Figure 2.7 Two-dimensional NMS solution representing differences in species assemblage between early- and late-season species in 1998 undisturbed forest types (R^2_{tot}=0.86, stress=11.1%, p=0.02) (N=48).

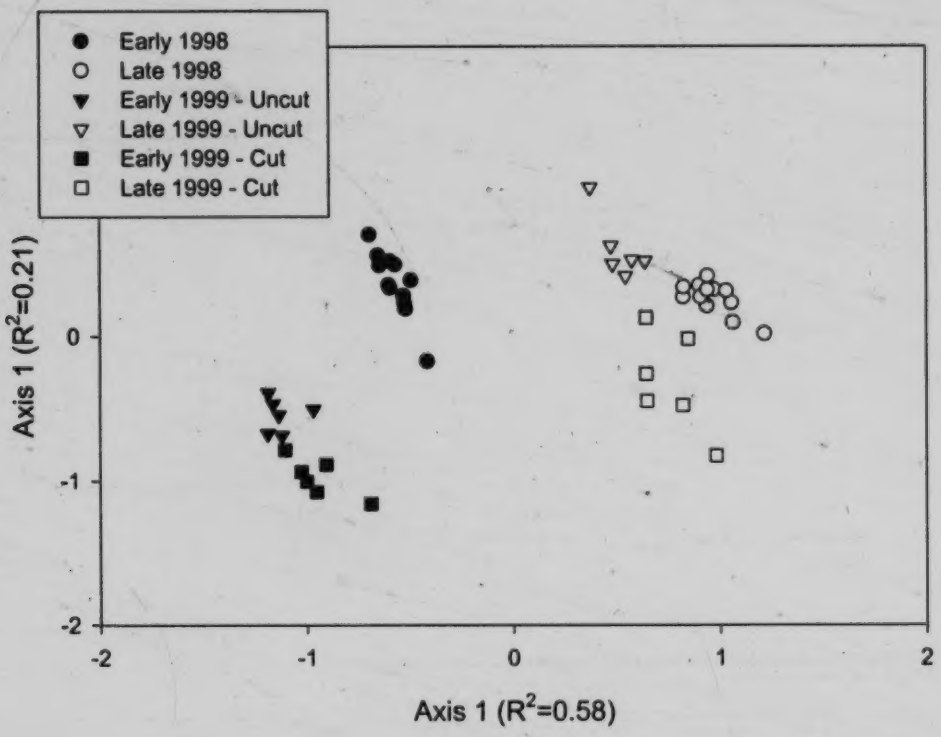

Figure 2.8 Two-dimensional NMS solution representing differences in species assemblage between early- and late-season species, pre- and post-harvest (R^2_{tot}=0.79, final stress=9.9%, p=0.03) (N=48).

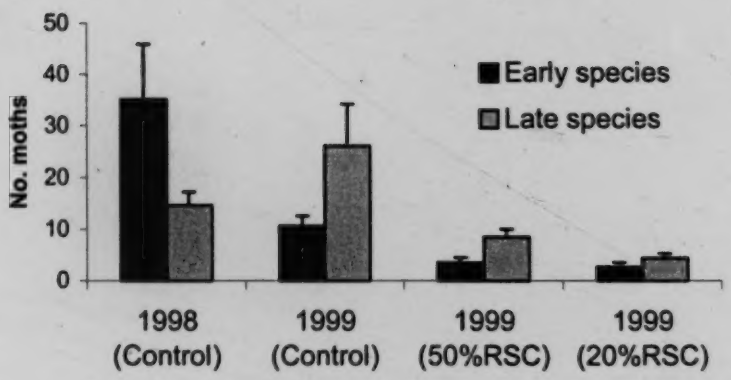

Figure 2.9 Mean trap catch (±SE) for early- and late-season moth species.

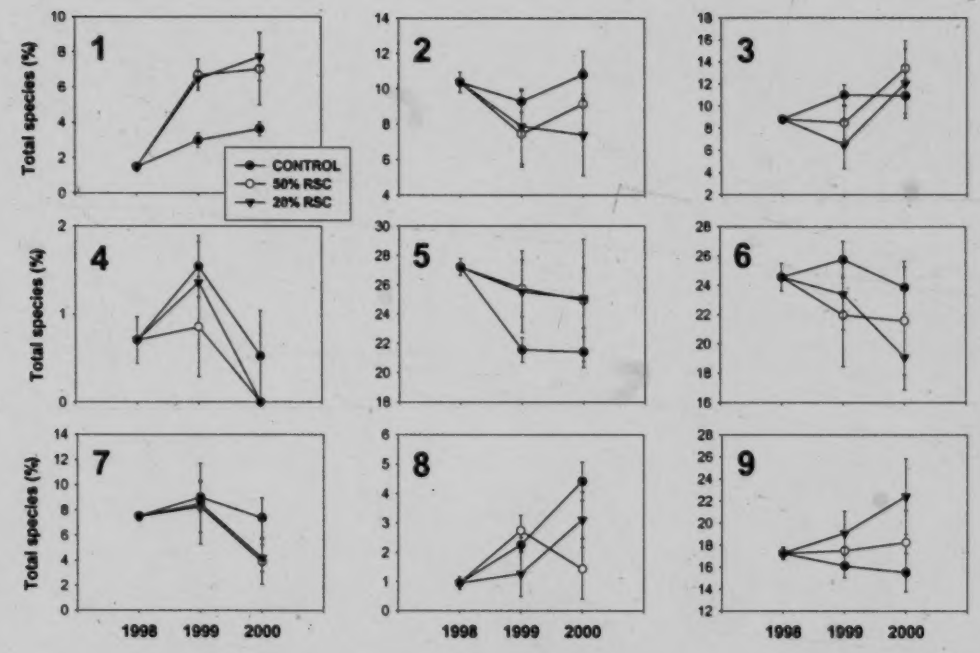

Figure 2.10 Percentage (±SE) of moth species in each feeding guild by treatment from 1998 to 2000. Guilds are: 1. Grass feeders, 2. Woody plants generalists, 3. Low and non-woody plants generalists, 4. Fungus and dead leaves feeders, 5. Salicaceae (poplars & willows) specialists, 6. Deciduous trees feeders, 7. Conifer feeders, 8. Lichen feeders, and 9. Generalists.

Chapter 3

Larval defoliator communities in trembling aspen (*Populus tremuloides* Michaux) and white spruce (*Picea glauca* (Moench) Voss) canopies before and immediately after partial cutting

3.1 Synopsis

The community of larval lepidopterans using canopy trees was assessed by whole-tree sampling of trembling aspen and white spruce in northern Alberta before and immediately after stands were logged (1998-1999) with two different levels of green-tree retention. Analysis of variance is used to compare defoliator abundance and diversity among logging treatments [20, 50 and 100% (unharvested control) of trees left on site] and forest types [deciduous dominated, deciduous with a spruce understory (mixed) and conifer dominated]. We paid special attention to potential forest pests. The community differed considerably between trembling aspen and white spruce canopies, yet was dominated by tortricid pests [*Choristoneura conflictana* (LAT) on aspen; *Choristoneura fumiferana* (SBW) and *Zeiraphera unfortunana* (PSS) on spruce] in addition to the geometrid *Operophtera bruceata* (BSW) on aspen. Significantly higher larval abundance per tree characterized conifer dominated stands and higher richness characterized deciduous dominated stands in comparison to mixed stand. More PSS and SBW larvae were found on spruce trees in control sites than on trees left behind in 20% residual structure compartments. No difference was found on aspen in response to logging in the

first year after logging. Stand composition, stand structure and environmental conditions offer explanations for differences among cover types and treatments.

3.2 Introduction

Defoliators contribute to important forest processes such as nutrient cycling (Seastedt and Crossley 1984) and community development (Schowalter *et al.* 1986). They may also regulate forest primary production (Mattson and Addy 1975). However, outbreaks of a few species (1-2%) of forest defoliators (Hunter 1991) are also a major cause of wood fibre losses in the western boreal forest (Volney and Mallet 1998). Forest entomological research to date has concentrated on these few 'pest' species and, unfortunately, only a limited amount of information is available on the great majority of non-pest species (Danks and Foottit 1989). Nonetheless, such information is critical to include defioliator communities in broad-based assessment of how industrial forestry affects biodiversity, especially in the boreal mixedwood forests of western Canada where forestry activities have been rapidly expanding over the past two decades (Lieffers and Beck 1994).

Until recently forest practices and policies worked against maintaining mixed stands on the western boreal landscape: conifer stands were planted with conifers and stands classed as deciduous dominated were left to regenerate mainly by aspen suckering (Lieffers *et al.* 1996). Today, as forest companies move toward sustainable, ecosystem-based management, there is

renewed interest in maintaining and creating mixedwood stands. It is thought that mixed composition and structure promote ecological diversity and other benefits such as improved long-term soil fertility, reduced susceptibility to pests (Franklin *et al.* 1989), increased productivity (Lieffers *et al.* 1999) and improved economic yield (Burkhart and Tham 1992). However, new mixedwood silvicultural systems (Lieffers *et al.* 1996) are being developed without much attention to potential pest activity of defoliators in mixed stands. On one hand, stress from partial cut harvesting, for example, might facilitate buildup of defoliator populations as population growth is inversely related to host plant vigor (Mattson and Addy 1975; Mattson and Haack 1987). On the other hand, silvicultural strategies that promote high ecological complexity may bolster the resilience of forest ecosystems and increase their ability to absorb stresses (Franklin *et al.* 1989). In an effort to resolve these general questions, we investigated impacts of partial harvesting on lepidopteran defoliators (i.e. caterpillars) using the two major commercial tree species in northern Alberta i.e. trembling aspen (*Populus tremuloides* Michaux) and white spruce (*Picea glauca* (Moench) Voss) in the boreal mixedwood forest.

The experiment objectives were to 1) identify larval defoliators associated with canopy trees of trembling aspen and white spruce in three forest types at the EMEND study site and 2) to investigate immediate impacts of partial cutting on defoliators. These objectives were addressed by replicated whole-tree sampling of defoliator communities during the summer seasons

immediately before and after disturbance by winter logging. The following hypotheses were formulated:

1. Species assemblages in the canopy will differ between trembling aspen and white spruce, two very different food plants, as many oligophagous species feed more efficiently on certain plants and are thus able to overcome plant defenses (Young 1997). Both tree species, even in a mixedwood setting, will have their own communities of defoliators, sharing only a few polyphagous species.
2. Partial cutting will have an immediate negative impact on species richness and abundance of defoliators compared to uncut sites due to post-harvesting environmental changes (e.g. increased air movement, removal of host trees, predation and parasitism).

3.3 Material and methods

3.3.1 EMEND Site and Study Design

This project was conducted under the umbrella of EMEND (Ecosystem Management by Emulating Natural Disturbance) (Spence *et al.* 1999), a large-scale multidisciplinary harvest-silviculture experiment in the boreal mixedwood forest of Alberta, 85 km northwest of Peace River (56°44'N, 118°20'W). The site is in the Lower Foothills natural subregion (Beckingham *et al.* 1996) of the Boreal Forest region (Rowe 1972) characterized by trembling aspen, balsam poplar, *Populus balsamifera* L., white spruce and black spruce, *Picea mariana*

(Miller) B.S.P. (Johnson *et al.* 1995). Vegetation in the area grows on fine-textured luvisolic soils (B. Kishchuk, personal communication).

Sites were selected according to forest type, treatment type, compartment shape and accessibility. Each compartment was 8-10 hectares in size. Different partial cutting levels were chosen to investigate commercial alternatives to clearcutting. See Volney *et al.* (1999) for more details on the overall experimental design.

3.3.2 Sampling

Trembling aspen and white spruce with height and diameter chosen to represent something close to the average for the stand were sampled over two years in three forest types (Figure 3.1): deciduous dominated (>70% trembling aspen and balsam poplar), conifer dominated (>70% conifer, mainly white spruce), and deciduous dominated with a strong white spruce understory (30-70% of canopy height), also called 'mixed' here for simplicity. Canopy aspen trees were felled in three deciduous dominated compartments in both years and in one mixed compartment in 1999. This last compartment was added to investigate stand composition effect on defoliators. Canopy spruce trees were felled in three conifer dominated compartments in each year and understory spruces in three mixed compartments in 1998 to investigate stand structure and composition effects on defoliators. A total of 33 aspen and 54 spruce were sampled. Aspen trees were felled from July 23 to July 26 in 1998 and from May 29 to June 10 in 1999. Spruce trees were felled in two bouts in 1998 from June

8 to June 19 and July 9 to July 17 and from June 20 to June 24 in 1999. All trees were felled on a 30' X 50' plastic tarp laid out on the forest ground. Tree crowns were stratified immediately after felling into lower, middle, and upper parts. Branches were then randomly selected in each crown level (two branches per level for aspen and ten 45-cm branch tips per level for spruce) and processed in a beating box (plastic recycling box) to shake off defoliators. The sample branches were also examined for defoliators in rolled and tied leaves, and for eggs, and pupae. Both the tree residuals and tarp were searched for a one-hour period for additional defoliators. Defoliators from branches and tarp were pooled and taken to the field laboratory for identification and rearing. Sampling was focused during a short period of time for each tree species as defoliator abundance and richness can change rapidly during growing season of trees.

3.3.3 Laboratory work

Defoliator larvae were reared in groups on fresh foliage in clear plastic cups at the EMEND field laboratory to obtain adults with known larval and host associations and parasitoids. A photographic record of associated larvae and adults was developed in 1998 and larvae were reared in 1999 only when it was deemed necessary to positively identify the species. Larvae were sorted initially to morphospecies based on external characters and host tree to construct representative, single-species rearing groups. Identifications were made mainly using Ives and Wong (1988), Wagner *et al.* (1997) and

photographed images of known species housed at the Northern Forestry Centre (Canadian Forest Service, Edmonton, Alberta, Canada). Voucher specimens were deposited in the NoFC arthropod collection.

3.3.4 Light trapping catches

Light trapping data has been used to estimate larval abundance of forest pests such as the SBW and, from this information, to predict outbreaks (Simmons and Elliot 1985). Light trap catches of certain pests were available from the EMEND site (Chapter 2). These were compared with the larval abundances established in this study to evaluate the strength of the relationship between light trap catches and larval abundance in the same stand.

3.3.5 Analyses

One-way analyses of variance (Zar 1996) were conducted on data about defoliator numbers and species richness by compartment, treatment and pest species using SAS version 8.0 (1999). Compartments were taken into account by using nested design inside each cover type. Data met the assumptions of normality and homogeneity of variance as required to interpret the F-ratio tests. Scheffe's multiple comparison test was used to examine significant differences between means from the ANOVA because it is conservative and does not require equal sample size (Zar 1996).

3.4 Results

Many individuals were collected both on the tarp and on the foliage. Defoliators from both sources included a similar distribution of species and so data were pooled for the analyses.

3.4.1 Lepidopteran defoliators diversity and dominance

Sampling forest canopy using whole tree harvesting resulted in a large collection of lepidopteran defoliators (Table 3.1). A total of 30 species from nine families were identified from aspen rearings (Table 3.2) and another 23 species from six families were identified from spruce rearings (Table 3.3). Overall, both aspen and spruce defoliator communities were dominated by tortricids and geometrids, in terms of abundance. Many of the most abundant species are known to be potential pests.

Purplestriped shootworms, *Zeiraphera unfortunana* Powell, accounted for 56% of the individuals collected from spruce in 1998 followed, in order of abundance, by *Coleotechnites atrupictella* (Dietz) (10%), eastern blackheaded budworms, *Acleris variana* Fern. (8%), and spruce budworms, *Choristoneura fumiferana* (Clem.) (2%). In 1999, 33% of the individuals collected on spruce were *Z.unfortunana*, 29% were *C.fumiferana*, 9% were *C.atrupictella* and 8% were redstriped needleworms, *Epinotia radicana* (Heinr.), which had represented only 1% of the larvae collected in 1998. No *A.variana* larvae were collected in 1999.

The community differed conspicuously on trembling aspen. In 1998, 70% of the individuals were unknown sp.1 while Canadian tiger swallowtails, *Papilio canadensis* (R.&J.), and two-lined aspen loopers, *Lobophora nivigerata* Wlk., accounted for 6% and 5% of the individuals, respectively. In 1999, Bruce spanworms, *Operophtera bruceata* (Hulst) (59%) and large aspen tortrix, *Choristoneura conflictana* (Wlk.) (39%) were strikingly dominant, representing 98% of all individuals collected. Only a few forest tent caterpillars, *Malacosoma disstria* Hbn., were collected in 1999 (Table 3.2).

C.conflictana and the green aspen leaftier, *Pandemis canadana* Kft., were the only species, with 2 individuals each, collected on both spruce and aspen. Neither species were successfully reared on spruce foliage.

3.4.2 Defoliator species richness

Species richness of aspen defoliators was similar among deciduous dominated compartments in 1998 (Table 3.4). Species richness was also similar on spruce, both among compartments and cover types. After partial cutting (1999), species richness on aspen was similar among treatments but differed significantly between the two cover types (Table 3.5). More species were collected in all three deciduous dominated stands compared to the mixed stand in 1999 (Figure 3.2).

On spruce, no statistically significant difference in richness could be demonstrated although results were close to significance among treatments

(p=0.07) with trees from the two partially cut treatments tending to have a lower number of species.

Species richness differed significantly between years on aspen as shown by comparison between control compartments (Table 3.6). More defoliators were captured per aspen tree in control compartments in 1999. In contrast, no similar difference was found on spruce between years (Table 3.7).

3.4.3 Defoliator abundance

There were no significant differences among deciduous dominated compartments in defoliator abundance on aspen in 1998 (Table 3.4). On spruce, however, a significant difference was found between the two cover types with defoliator abundance much higher on canopy spruce in the spruce dominated stands than on understory spruce beneath a deciduous canopy (Figure 3.3). Interestingly, there was not any striking difference in larval abundance on spruce trees in compartments of each cover type.

A difference was noted among treatments in number of individuals collected on aspen in 1999 (Table 3.5). More specimens were collected from trees in control and 20% residual compartment than from those in the intermediate 50% residual treatment (Figure 3.2). No strong differences were exhibited among cover types. On spruce, however, there was no difference in abundance among different treatments although controls tended to have more defoliators than partially harvested compartments (Figure 3.2). Finally, there was a significant difference in abundance between 1998 and 1999 on aspen

(Table 3.6) but there was no difference in abundance between years on spruce (Table 3.7).

3.4.4 Abundance of particular forest pests

Analyses of the whole larval lepidopteran fauna could hide species-specific responses if different species react differently to either stand composition (cover types) or treatments. Sporadic, uncommon species make up a large portion of the species richness but are a small fraction of the total defoliator abundance. We selected the two most abundant species on each tree species for more detailed study. Two major pests of aspen, *C.conflictana* (LAT) and *O.bruceata* (BSW), were not affected by treatment in a measurable way in 1999 (Figure 3.4). However, LAT was significantly more abundant on aspen in deciduous dominated stands than in the mixed stand (Figure 3.4). Interestingly, BSW exhibited the opposite pattern as it was significantly more abundant on aspen in the mixed than in deciduous dominated stands. Larvae of neither of these two species were collected in 1998 on aspen.

In 1998, the two most common pests of spruce, *C.fumiferana* (SBW) and *Z.unfortunana* (PSS), were significantly more abundant in conifer dominated stands than in the mixed stand (Table 3.8). PSS exhibited significant spatial variation, being found more abundantly in compartment 918 compared to the others and this compartment experienced a small outbreak of PSS that extended into summer 1999. During 1999, however, PSS was less abundant in the more severe partial cutting compartment (20% residual structure) compared

to the control (Figure 3.5). SBW followed the same trend, however, the differences were not statistically significant. The high numbers of PSS caterpillars in the control site from the outbreak pocket detected in 1998 accentuated differences among compartments and probably drove the latter significant difference.

Data from EMEND light traps were available for LAT and SBW (Table 3.9). LAT catches soared in 1999 and 2000 compared to 1998. SBW catches remained low on all years. Catches suggested a relationship with high larval abundance of LAT per tree in 1999 (Figure 3.4; Table 3.2) and low larval abundance of SBW per tree over two years (Figure 3.5; Table 3.3).

3.5 Discussion

No study has been published, to our knowledge, on impacts of partial cutting and lepidopteran defoliators. Our results might thus provide new insights on the response of Lepidoptera to forestry activities. Moths at EMEND were quite similar among aspen, spruce, and mixed stands. However, only a small proportion of them collected by light trapping used main canopy trees as host in their larval stage (Chapter 2). This implies that overall plant diversity in these stands is highly important and should be considered for this type of study. We found that aspen and spruce had markedly different faunas. There was also a trend toward loss of per tree caterpillar numbers with partial cutting.

Finally, lower defoliator diversity was found in mixed forest sites compared to pure forest sites. These issues are more fully discussed below.

3.5.1 Diversity and dominance

Defoliator communities differed on aspen and spruce, as hypothesized, because many lepidopteran species are restricted to a narrow range of food plants (Young 1997) and aspen and spruce are very different plants in terms of foliage chemistry (Yarie and Van Cleve 1994). LAT and *P.canadana* were the only species collected on both tree species with only two individuals found on spruce. The larvae must have been wanderers because these species are known to feed mostly on trembling aspen.

Dominant species in the larval community during both years were mostly tortricid pest species and one common geometrid species (BSW) with pest potential. This is not surprising, as these species are often numerous and many of them express outbreak dynamics in the western boreal forest (Ives and Wong 1988). For example, LAT and BSW dominated aspen defoliators on sampled trees. In 1999 and 2000, there was a general outbreak of these two species in the Peace River region (H. Ono, personal communication) that was well reflected in light trapping catches of LAT at EMEND. There was also an outbreak of forest tent caterpillar, *M.disstria*, in neighboring areas (Morneau, personal observation). Interestingly, few specimens of *M.disstria* were collected on sampled trees. These results on pests of surrounding areas and at EMEND

suggest that subtle variations in local weather are unlikely to significantly affect defoliators.

3.5.2 Richness and abundance between cover types

Aspen defoliator species richness differed between cover types. Contrary to my hypothesis, more species were found on aspen in deciduous dominated forest than in mixed forest on a per tree basis. A similar pattern for defoliator abundance occurred on spruce where mixed stands yielded, as expected, fewer defoliators from sampling than conifer dominated stands. The general result of fewer species in mixed stand could flow from a lower probability that female moths would find and exploit acceptable resources in mixed stand composition (Schowalter 1985). However, this is unlikely because no difference in moth species richness and trap catch was detected among cover types (Chapter 2). The spruce trees sampled in the mixed stand were part of the understory (30-70% canopy height) compared to dominant spruce in pure stands. Environmental conditions obviously differed between the understory than in the canopy and understory situations may be less suitable for folivore development. Canopies, for example, are warmer because they receive more solar radiation and larvae, which are poikilothermic, doubtlessly benefit from warm temperature by assimilating foliage more efficiently. Also, a bird study at EMEND suggested that relative abundance of foliage-gleaning birds were slightly more numerous in stands with a spruce component ($p=0.018$), probably using spruce as cover but also feeding on aspen

(B.Harrison, unpublished results). Therefore, differences in stand composition and structure are consistent with differences found between cover types.

3.5.3 Richness and abundance between years

Differences between years in abundance and species richness on aspen was due to two factors. Firstly, in 1998 sampling occurred later in the season than in 1999 and 1998 also was characterized an abnormally warm spring. A different community of late developmental feeders was sampled in 1998 because of the unintended phenological shift in sampling window. This may explain the significant between-year difference in overall numbers as the group of 'spring feeders' includes many outbreaking species (Hunter 1991). These are usually more numerous and part of a more diversified community than 'summer feeders', because spring feeders exploit young leaves that are more nutritious than old ones (Feeny 1970). A second reason for between-year differences in assemblage structure is the explosion of the LAT population in 1999 (as shown by light trapping catches for this species, Chapter 2). Thus, although we know that the aspen assemblage differed due to changes in relative abundance of this important defoliator, lack of phenological consistency in samples complicates interpretation of between-year differences.

For spruce assemblages, however, sampling dates were equivalent in both years. Lack of significant differences on spruce between years for both species richness and abundance is thus likely to be a valid result.

3.5.4 Effects of partial cut harvest

No significant difference in aspen defoliator abundance was detected among compartments in 1998 based on per tree data, perhaps due to variability among trees and overall small sample size. However, the data suggest that fewer defoliators were present in compartment 953 (Figure 3.3), a future 50% residual structure compartment (RSC) and this may have contributed to the drop in per tree abundance observed following harvest (Figure 3.2). On spruce, however, no between-year effect on the defoliator community was apparent among controls and, therefore, differences between treatments may be considered real. Partial cutting in spruce at either retention level were not associated with statistically significant change to larval lepidopteran assemblages, but the trends suggest immediate per tree reductions in larval lepidopteran abundance and diversity.

Changes in defoliator numbers following logging could come from at least five sources: 1) direct removal of defoliators from tree harvesting, 2) immigration of defoliators in the spring from the surrounding forest, 3) altered host condition (foliage nutrient and allelochemic content) due to stress caused by harvesting, 4) response of lepidopteran predators and parasitoids to logging and 5) environmental conditions in the residual canopy of thinned stands.

Direct removal of defoliator eggs, diapausing larvae, and pupae during winter logging will result in reduction of overall stand populations in proportion to the amount of host foliage left undisturbed after logging, i.e. there will be

more loss in 20% RSC than in 50% RSC. Defoliators, with stages overwintering in the understory, however, could also concentrate on residual trees. If this were a significant factor, more larvae would have been found on sampled tree in 20% RSC and 50% RSC compared to controls but this was not the case. Anticipated direct effects of lepidopteran removal are not reflected in our data and, thus, this factor is likely of minimum importance in explaining the patterns observed.

Stand manipulation could also influence dispersal and colonization by insects. Small larvae from surrounding forest could take advantage of increased air movement to disperse aerially and establish in thinned stands early in the spring. However, in contrast, Régnière and Fletcher (1983) suggested that thinning could reduce dispersal success of small SBW larvae and thereby reduce their population survival. Therefore, this factor should not have played an important role in generating the defoliator patterns seen in 1999.

Rapid growth of the defoliator population due to physiological changes in host trees in the year following disturbance is unlikely. It is well established that both quality and quantity of available nutritional resources are modified by thinning (Bauce 1996, Safranyik *et al.* 1998). Furthermore, stress through harvesting wounds and changed stand characteristics increases tree vulnerability to insects (Piene 1989) by lowering their ability to mount inducible defenses (Mattson and Haack 1987). Nonetheless, significant population

growth usually follows such disturbances only after several seasons of altered host condition (Schowalter 1985).

Predators and parasitoids of lepidopteran defoliators are also affected by logging (Schowalter *et al.* 1981) and such impacts could promote rapid changes in population numbers. More rapid development resulting from higher temperature in thinned stands may decrease impact of natural enemies (e.g. invertebrate predators) on defoliators (Parry *et al.* 1998). Also, preliminary results of a parasitism study conducted at EMEND showed lower parasitism rate in 20% RSC compared to 50% RSC and controls (J. Dunlop, personal communication). In our case, however, per tree defoliator populations went down with the amount of residual structure left per compartment. Other predators such as bird and small mammal could have influenced defoliator populations. For example, MacKenzie and Mahon (1998) in British Columbia showed that partial cutting with 70% and 40% residual structure retained a significant proportion of bird and small mammal assemblages from uncut forest and increased abundance of certain species typical of clearcuts. We suggest that the ratio of vertebrate predator to lepidopteran defoliator might have increased with thinning intensity. This change might partly explain the per tree decrease in defoliators seen in partially cut compartments.

Manipulating stand structure by thinning will affect most insects by modifying microclimate inside a stand through factors such as increased air circulation, higher volume of precipitation reaching the ground, and increased

temperature due to a greater amount of solar radiation penetrating the stand. Environmental conditions could be beneficial to defoliator larvae developing in more open stands as higher temperature is associated with increased spring development rates of SBW (Bauce 1996) and spruce budmoth, *Zeiraphera canadensis* Mut. & Free. (Régnière and Turgeon 1989). Our data, however, showed that countervailing forces made thinning detrimental overall to defoliators one year post-harvest. Fluctuating temperatures, low humidity, and high winds could have made the microclimate within the canopy of more isolated trees harsher than the closed canopy tree microclimate and, thus, limit population growth of canopy arthropods (Ozanne *et al.* 2000).

Despite the fact that the before-after comparison is somewhat confounded by use of different phenological sampling windows, comparison of uncut controls with partial cutting treatments using the 1999 data suggest a significant effect. More larvae were present on trees in control compartments and 20% RSCs than on trees in the 50% RSCs. The data from 1998 suggest that fewer defoliators were present in the 50% RSC before treatments were applied. Therefore, the significant difference demonstrated probably reflects only a lower starting level for defoliator populations in the 50% RSC compared to other compartments. Thus, it seems safe to conclude that partial cutting caused no immediate changes in abundance or diversity of the aspen defoliator community.

3.5.5 Response of forest pests

Species that were numerous and known to be potential pests with outbreak dynamics were good candidates for looking at species-specific abundance patterns. These species coexist in the same habitat as non-outbreaking species. However, they can respond to changes in their habitat in an eruptive way (Hunter 1991). Thereby it is important to understand their response to forest stand manipulations such as partial cutting if economically viable alternatives to clearcutting sought by forest companies are to be developed.

LAT and BSW showed no response to treatment immediately following partial cutting in the aspen compartments. In contrast, the 20% RSC spruce compartments showed significantly lower population of PSS in comparison to control compartments. SBW followed the same trend seen in PSS but the differences were not significant. We suggest that these spruce defoliators in conifer dominated stands are more negatively affected immediately following thinning treatments than were aspen defoliators in deciduous dominated stands. The latter species experience considerable environmental changes annually in the leaf flush and fall cycle of deciduous canopies that are more open naturally than those of spruce. In contrast, spruce defoliators have evolved in stands where trees keep their foliage all-year long. Their environment is thus more constant in terms of air circulation, moisture, and solar radiation. Therefore, partial cutting might have had a greater negative

impact on spruce species by opening up the stand canopy. We hypothesize that eggs (e.g. PSS) and early-instar larvae (e.g. SBW) of spruce defoliators suffer increased spring losses in thinned stands.

3.6 Conclusion

Lepidopteran assemblages differed conspicuously between aspen and spruce, even when they were growing in mixed stands. Thus, understory spruce may be somewhat protected from defoliator damage when growing beneath an aspen canopy and defoliator communities on mature spruce must develop mainly after these trees have broken into the canopy. In general, only a small immediate impact of partial cutting on the defoliator community was detected and this was concentrated in spruce stands where populations of pest species like *Z. unfortunata* and *C. fumiferana* appear to be negatively affected.

As these partially cut stands develop, we anticipate further effects on lepidopteran larval assemblages using the canopy. Defoliator larvae in partially cut compartments will develop faster and eat more foliage on trees that have more foliage (Bauce 1996) in the first few years. Such larvae will show increased pupal weight and fecundity and will have higher survival rates (Bauce 1996; Bauce and Carisey 1996). After a few years, an increase in tree vigor (Safranyik *et al.* 1998) will hold most defoliators at endemic population levels. Long-term impact of herbivory will be reduced due to compensatory growth by surviving trees, similar to that following insect-related mortality (McNaughton

1983). An increase in biodiversity will most likely be seen caused by an increase in plant diversity and stand structure over time (Southwood *et al.* 1979). This spatial and temporal heterogeneity will allow stands to harbor more species. Long-term studies to follow the behavior of defoliators associated with tree recovery after thinning will help choose forestry practices that discourage population growth of defoliators and meet the goals of sustainable forest management.

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Table 3.1 Total number of trees sampled, defoliator larvae collected and defoliator species collected on the EMEND site in 1998 and 1999.

	No. trees	Total larvae	Larvae reared
1998			
Trembling aspen	9	86	86
White spruce	36	993	993
1999			
Trembling aspen	24	3006	371
White spruce	18	277	118

Table 3.2 Abundance of lepidopteran defoliators reared on trembling aspen over two years.

	1998	1999
Tortricidae		
Acleris obtusana (Evers.)	1	0
Apotomis dextrana (McD.)	0	3
Choristoneura conflictana (Wlk.)	0	1176
Choristoneura rosaceana (Harr.)	0	3
Epinotia criddleana (Kft.)	0	21
Epinotia nisella (Cl.)	0	6
Epinotia solandriana (L.)	0	1
Pandemis canadana Kft.	0	1
Pandemis limitata (Rob.)	0	13
Pseudosciaphila duplex (Wlsm.)	1	0
Gelechiidae		
Anacampsis niveopulvella (Cham.)	0	1
Oecophoridae		
Depressariodes ciniflonella Lienig & Zell.	0	1
Papilionidae		
Papilio canadensis (R. & J.)	5	0
Geometridae		
Campea perlata (Gn.)	0	1
Itame loricaria (Evers.)	0	4
Lobophora nivigerata Wlk.	4	0
Metanema inatomaria Gn.	1	0
Operophtera bruceata (Hulst)	0	1763
Lasiocampidae		
Malacosoma disstria Hbn.	0	13
Phyllodesma americana (Harr.)	1	0
Notodontidae		
Clostera brucei (Hy. Edw.)	1	0
Furcula scolopendrina (Bdv.)	1	0
Gluphisia septentrionis Wlk.	1	0
Arctiidae		
Platarctia parthenos (Harr.)	0	1
Noctuidae		
Autographa ampla (Wlk.)	0	1
Egira dolosa (Grt.)	0	4
Enargia infumata (Grt.)	0	111
Graphiphora augur (F.)	0	1
Ipimorpha pleonectusa Grt.	0	1
Pyrrhia experimens (Hufn.)	2	0

Table 3.3 Abundance of lepidopteran defoliators reared on white spruce over two years.

	1998	1999
Tortricidae		
Acleris variana (Fern.)	79	0
Archips striana (Fern.)	1	0
Choristoneura conflictana (Wlk.)	0	2
Choristoneura fumiferana (Cl.)	22	81
Epinotia radicana (Heinr.)	9	21
Pandemis canadana Kft.	2	0
Zeiraphera fortunana (Kft.)	1	0
Zeiraphera unfortunana Powell	551	92
Gelechiidae		
Coleotechnites atrupictella (Dietz)	96	25
Geometridae		
Caripeta divisata (Wlk.)	11	0
Cladara limitaria (Wlk.)	28	0
Eupithecia annulata (Hulst)	9	0
Eupithecia luteata Pack.	1	0
Ectropis crepuscularia (D. & S.)	1	0
Epirrita autumnata (Bkh.)	1	0
Macaria signaria dispuncta (Wlk.)	5	0
Arctiidae		
Eilema bicolor (Grt.)	9	0
Lymantriidae		
Dasychira plagiata (Wlk.)	7	0
Noctuidae		
Feralia jocosa (Gn.)	6	0
Idia americalis (Gn.)	1	0
Platypolia anceps (Steph.)	0	1
Syngrapha rectangula (Kby.)	0	1
Syngrapha viridisigma (Grt.)	1	0

Table 3.4 ANOVA table of aspen and spruce defoliator species richness and abundance in undisturbed forest (1998).

Source of variation	d.f.	MS	F	P
ASPEN 1998				
Richness				
Compartment	2	10.78	1.49	0.298
Error	6	7.22		
Abundance				
Compartment	2	8912.33	1.00	0.421
Error	6	8896.89		
SPRUCE 1998				
Richness				
Cover type	1	6.25	0.29	0.595
Compartment	4	10.06	0.47	0.760
Error	30	21.59		
Abundance				
Cover type	1	11772.25	6.55	0.016*
Compartment	4	4316.67	2.40	0.072
Error	30	1796.06		

Table 3.5 ANOVA table of aspen and spruce defoliator species richness and abundance following partial cutting treatments (1999).

Source of variation	d.f.	MS	F	P
ASPEN 1999				
Richness				
Cover type	1	22.22	9.20	0.007*
Treatment	2	5.39	2.23	0.134
Error	20	2.42		
Abundance				
Cover type	1	10804.50	2.76	0.112
Treatment	2	16420.67	4.20	0.030*
Error	20	3908.70		
SPRUCE 1999				
Richness				
Treatment	2	21.56	3.11	0.074
Error	15	6.92		
Abundance				
Treatment	2	402.89	2.34	0.132
Error	15	172.52		

Table 3.6 ANOVA table of between-year (1998 vs. 1999) aspen defoliator species richness and abundance in untreated deciduous dominated stands.

Source of variation	d.f.	MS	F	P
Richness				
Year	1	86.04	14.18	0.002*
Error	13	6.07		
Abundance				
Year	1	1568952.10	81.63	<0.001*
Error	13	19219.45		

Table 3.7 ANOVA table of between-year spruce defoliator species richness and abundance in untreated coniferous dominated stands.

Source of variation	d.f.	MS	F	P
Richness				
Year	1	0.06	0.00	0.960
Error	22	21.44		
Abundance				
Year	1	2415.13	0.75	0.395
Error	22	3213.71		

Table 3.8 ANOVA table of the abundance of four common forest pests on trembling aspen and white spruce.

Source of variation	d.f.	MS	F	P
ASPEN 1999				
Operophtera bruceata (Hulst)				
Cover type	1	95484.50	6.29	0.021*
Treatment	2	8925.17	0.59	0.565
Error	20	15175.1		
Choristoneura conflictana (Clem.)				
Cover type	1	80668.06	5.17	0.034*
Treatment	2	17636.72	1.13	0.343
Error	20	15614.32		
SPRUCE 1998				
Choristoneura fumiferana (Clem.)				
Cover type	1	10.89	5.44	0.038*
Compartment	4	0.56	0.28	0.887
Error	12	2.00		
Zeiraphera unfortunana Powell				
Cover type	1	15960.89	33.82	<0.001*
Compartment	4	8456.06	17.92	<0.001*
Error	12	471.74		
SPRUCE 1999				
Choristoneura fumiferana (Clem.)				
Treatment	2	18.72	2.17	0.1488
Error	15	8.63		
Zeiraphera unfortunana Powell				
Treatment	2	134.00	4.51	0.0293*
Error	15	29.73		

Table 3.9 Light trap catches of common forest pests at EMEND over three years by host tree.

Pest species by host	1998	1999	2000
Trembling aspen			
Choristoneura conflictana (Clem.)	63	1151	3257
Malacosoma disstria Hbn.	14	217	24
White spruce			
Choristoneura fumiferana (Clem.)	29	40	13

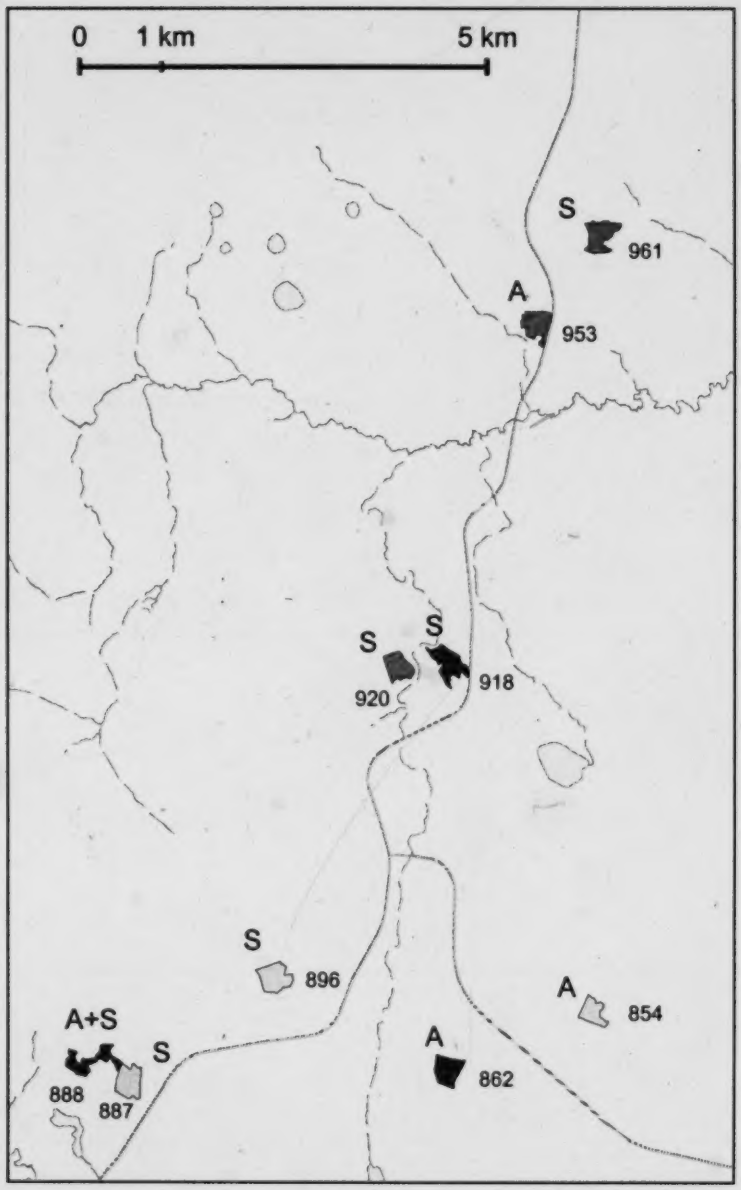

Figure 3.1 EMEND map showing compartments used for tree sampling (A for aspen, S for spruce; control in black, 50% residual in dark grey and 20% residual in light grey), roads and streams.

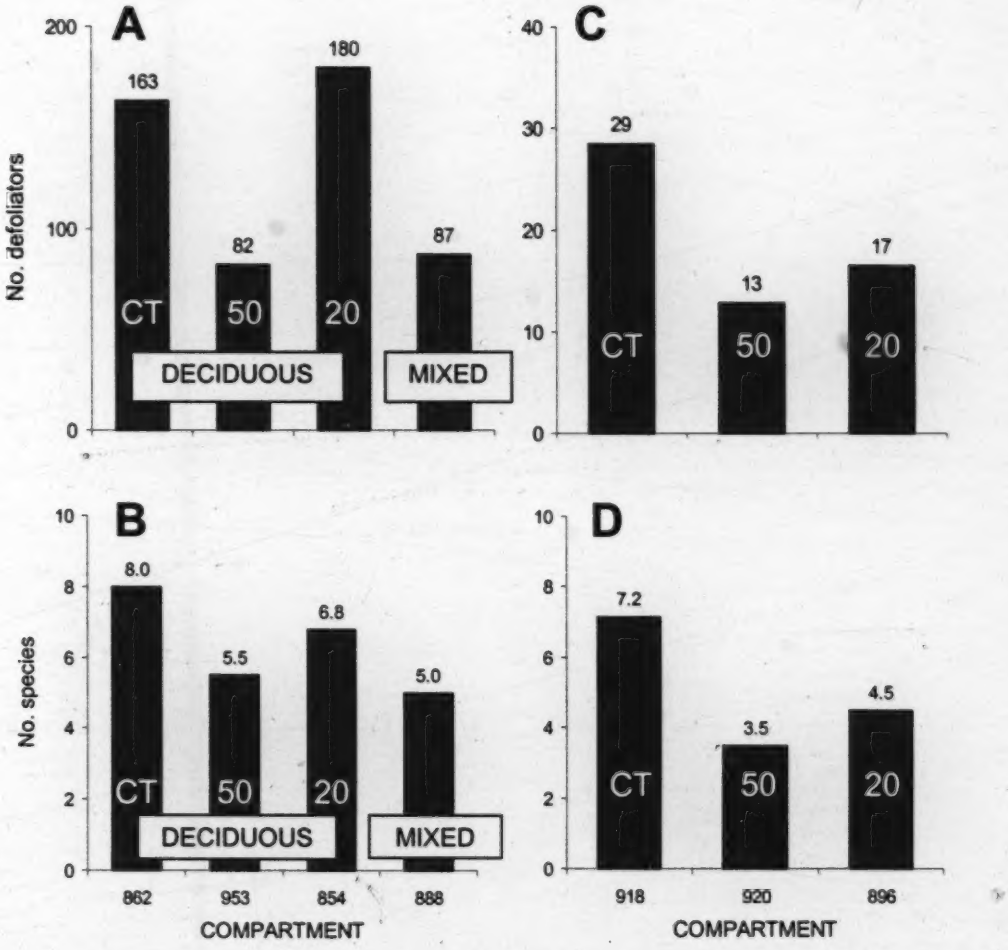

Figure 3.2 1999 defoliators. Mean abundance (A) and species richness (B) on aspen per tree in four compartments (N=24). Mean defoliators abundance (C) and species richness (D) on white spruce per tree in three compartments (N=18). Treatments are indicated on each bar (CT: control, 50: 50% residual structure, 20: 20% residual structure).

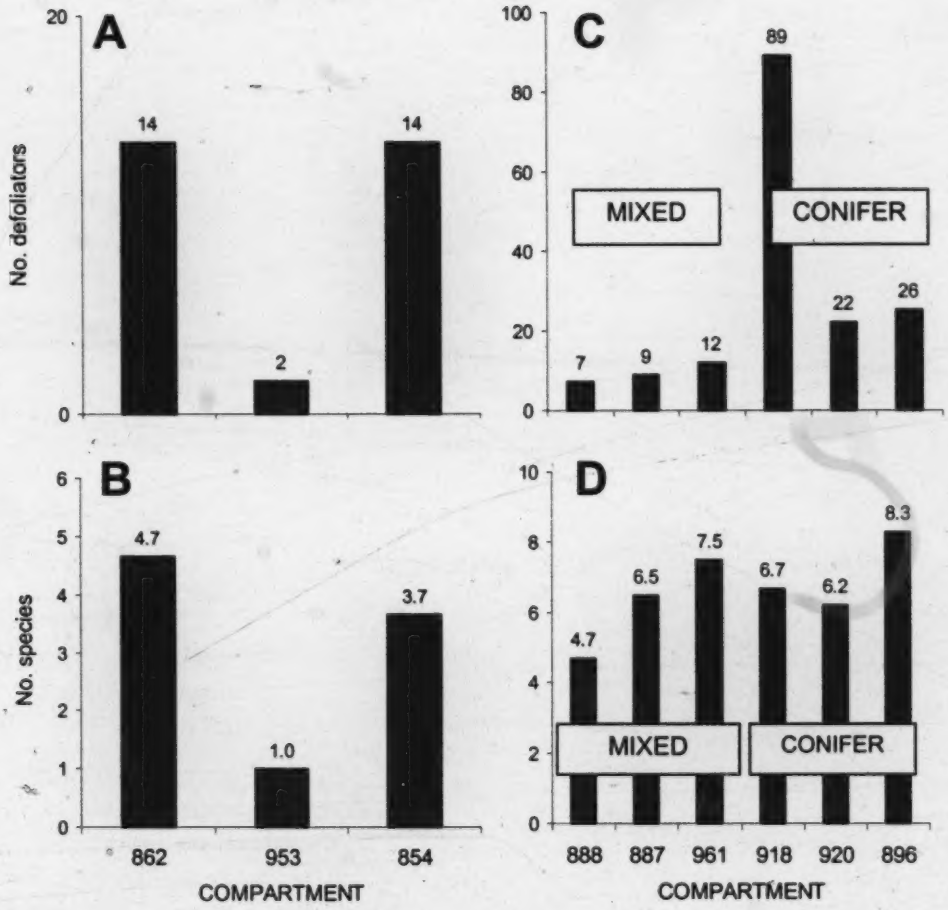

Figure 3.3 1998 defoliators. Mean abundance (A) and species richness (B) on aspen by tree in three compartments (N=9). Mean abundance (C) and species richness (D) on spruce per tree in six compartments (N=36).

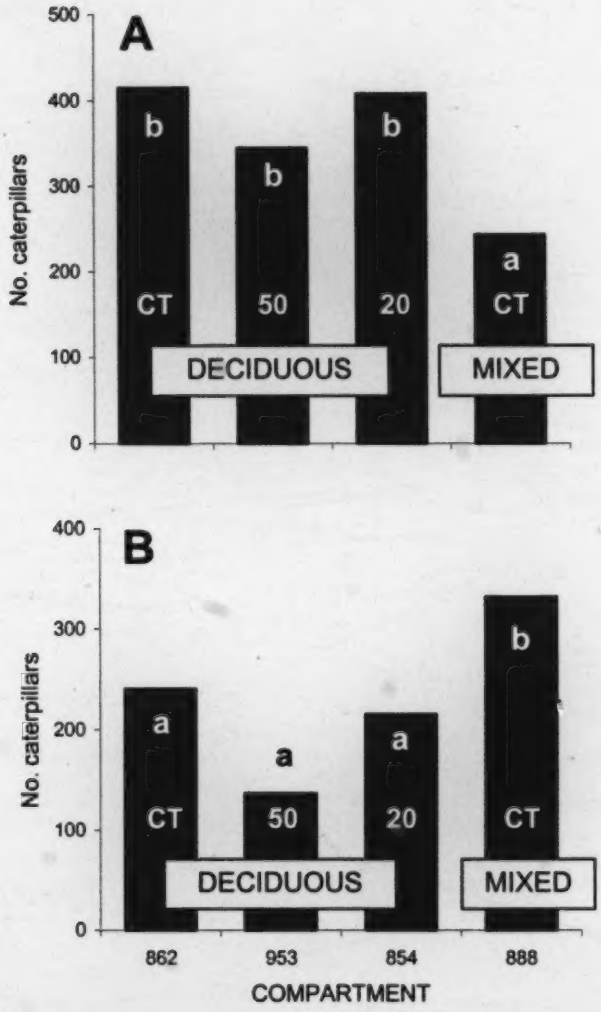

Figure 3.4 Mean abundance per cover type and treatment of (A) Bruce spanworm, *O.bruceata,* and (B) large aspen tortrix, *C.conflictana,* from 1999 tree sampling conducted at EMEND (N=24). Bars with the same letters are not significantly different (Scheffé's test, $p<0.05$).

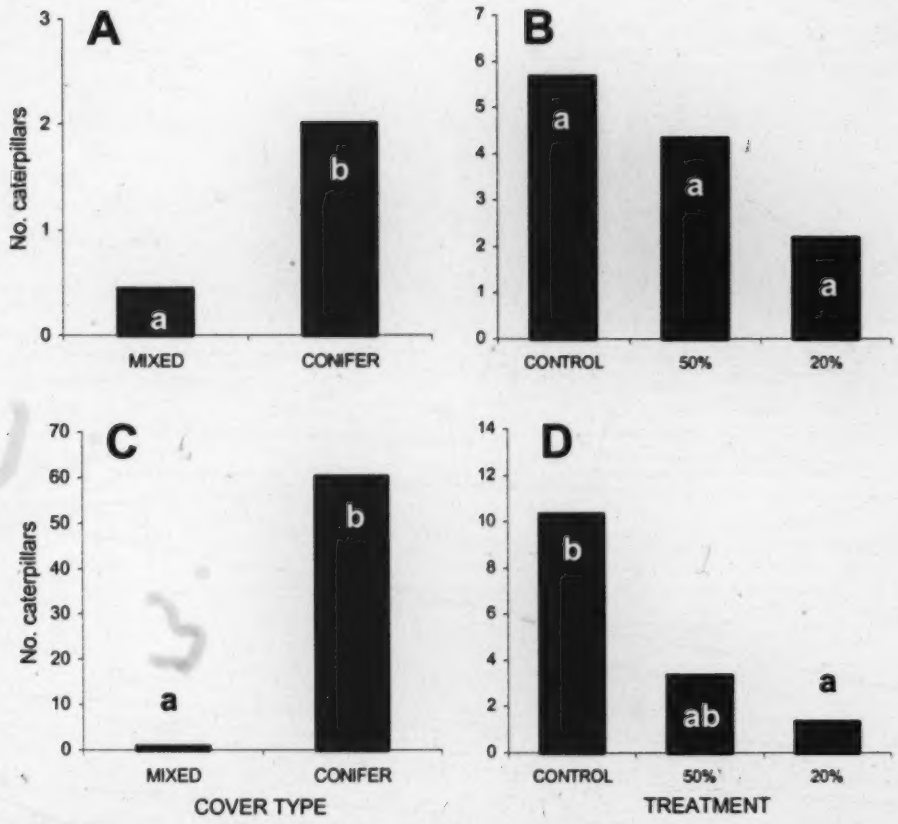

Figure 3.5 Mean abundance per cover type and treatment of (A) 1998 and (B) 1999 spruce budworm, *C.fumiferana*, and (C) 1998 and (D) 1999 purplestriped shootworm, *Z.unfortunana*, from tree sampling conducted at EMEND (N=18). Bars with the same letters are not significantly different (Scheffé's test, $p<0.05$).

Chapter 4

General Discussion and Conclusions

4.1 Partial cutting and moths

It is now recognized that what is good for wood production is not necessarily good for other forest organisms and processes (Franklin *et al.* 1989, Hunter 1991). Therefore, forest companies harvesting in the boreal mixedwood forest of Alberta have adopted a natural disturbance approach to forest management, based on the belief [as opposed to evidence (Spence 2001)] that leaving residual structure on harvested blocks might preserve biological diversity. However, recent studies have suggested that small residual clumps of trees might be inappropriate for many organisms: birds and small mammals (Andrén 1994), old-growth specialist carabids (Spence *et al.* 1996) and certain canopy arthropods (Ozanne *et al.* 2000). My thesis contributes to this issue by investigating the utility of green-tree retention for preserving the lepidopteran fauna associated with boreal mixedwood forest.

Lepidopteran assemblages have been widely used to investigate a wider range of questions about natural disturbances and forestry impacts. For example, a number of authors have used lepidopterans to investigate faunistic differences in forest types (Magurran 1985; Waring 1989; Robinson and Tuck 1993; Hammond and Miller 1998; Landau 1998; Work *et al.* 1998). In terms of response to disturbances, moth assemblages have been used to investigate the impacts of gypsy moth defoliation (Work and McCullough 2000), comparisons

between clear-cutting and wildfire (Chaundy 1998), and other disturbances (Kitahara and Fujii 1994). They have also been used to assess the utility of forest patches as habitats to maintain biota on a fragmented landscape (Usher and Keiller 1998) and impacts of forest decline on caterpillars (Martel and Mauffette 1997). Interest in these assemblages and their study has led scientists to consider the effects of trap location on moth catches (Thomas 1996), yearly fluctuations in catches related to life-history strategies (Rejmánek and Spitzer 1982), sampling strategies for estimating moth diversity (Thomas and Thomas 1994), and trap type and weather factors on light trap catches (Butler *et al.* 1999). Finally, there is a growing wealth of baseline data available for some forest types (e.g., Butler and Kondo 1991; Butler and Strazanac; Thomas 2001). However, no published study has used lepidopteran assemblages to address the current green-tree retention issue in forestry. My findings show that moths are indeed an interesting and useful group to investigate forest harvesting impacts in the boreal mixedwood forest. For moths studied by light trapping, I found that:

1. Species assemblages were similar across forest cover types. These results agree with those of Usher and Keiller (1998) in deciduous, coniferous, and mixed farm woodlands but contradict those of Waring (1989) who found a significant difference in moth assemblages between deciduous woodlands adjacent to coniferous woodlands resulting from changes in larval food plants. The relative homogeneity of understory vegetation composition at EMEND

probably explains the similarity in moths among cover types. Also, dominance of the moth community by habitat use generalists and polyphagous moth species, feeding mainly on common understory plants, created a major overlap of species between cover types, which might explain the similarity found among cover types.

2. Significant decreases in moth trap catch and species richness in residual structure compartments (RSC) demonstrated the immediate negative effect of partial cutting on moth populations. Moths were particularly affected in the 20% RSC. Changes in environmental conditions presumably caused this decrease by lowering site quality for moths (more wind, more extreme temperature, and less moisture). Changes in the plant community did not likely play a major role because many previous studies have demonstrated that it takes a few years before a plant community fully responds to disturbance (Halpern and Spies 1995; Peterson and Pickett 1995).

3. Moth populations responded differently to partial cutting, in ways perhaps correlated with differential mobility within families that seems to be rooted in structural characteristics (Woiwod and Stewart 1990). Harvest treatments negatively affected trap catch of Noctuidae, Geometridae, and Uraniidae and species richness of Geometridae and Notodontidae. These results partly highlight the potential of Geometridae as an indicator group of

environmental quality as suggested by Scoble (1992) based on their restricted mobility. Other studies have shown that geometrids 1) are neither strong fliers nor early colonizers following disturbance (Woiwod and Stewart 1990), 2) are positively related to plant species richness, patch size and shape in farm woodlands (Usher and Keiller 1998), and 3) have a lower proportion of migrants than other lepidopteran families (Young 1997). All these factors, in my opinion, contribute to making this family a very interesting and useful taxon for assessments of change following disturbance and for monitoring biodiversity as an indicator of ecosystem function.

4. Disturbance was beneficial to generalist, grass and pioneer plant feeders while detrimental to deciduous tree, conifer, woody plant and lichen feeders. These differences increased over two years after partial cutting suggesting that moth assemblages will change with time as the plant community responds to partial cutting. Effects were slightly more pronounced, expectedly, in 20% RSC than in 50% RSC due to greater structural changes and stand opening.

4.2 Partial cutting and caterpillars

The second part of the thesis dealt with larval defoliators in the canopy of trembling aspen and white spruce. My data showed that:

1. The caterpillar communities differed conspicuously between trembling aspen and white spruce. They were dominated by the tortricid pests *Choristoneura fumiferana* (SBW) and *Zeiraphera unfortunana* (PSS) on spruce and *Choristoneura conflictana* (LAT) on aspen in addition to the geometrid pest *Operophtera bruceata* (BSW) on aspen.

2. On average, lower defoliator abundance and, to a lesser extent species richness, were found on spruce and aspen in a mixed cover type compared to conifer- and deciduous-dominated cover types. Data for individual species showed more significant differences between mixed and pure cover-types than did overall defoliator data. Both SBW and PSS were less abundant in the mixed cover type (on understory spruce) compared to the conifer-dominated cover type (on overstory spruce) probably due to differences in crown microclimate and greater distance between host trees in the mixed cover type. On aspen, BSW was less abundant in mixed stands but LAT was more abundant there, suggesting effective generalizations about use of such cover-types will be restricted to the species level, at least for boreal lepidopterans.

3. Immediate impact of partial cutting on the whole defoliator community was not very strong and was concentrated on pests in spruce stands. The effects were directly related to the amount of residual structure. Defoliators were already overwintering in the stand when partial cutting was conducted.

Therefore, stronger effects of partial cutting are to be expected on Lepidoptera in the following year due mostly to environmental changes and altered host conditions of remaining trees (Schowalter 1985). The immediate negative trends seen for PSS and SBW in my data suggest the potential of partial cutting for pest management. Previous studies demonstrated, for SBW, that thinning should be avoided during an outbreak of the insect (Piene 1989) but could reduce the vulnerability of trees if conducted two years before an outbreak (Bauce 1996). Trends in my results corroborate these studies. Partial cutting at EMEND decreased per tree population of PSS and SBW and might thus be investigated as a new tool for pest management.

4. Pre-treatment variation in populations of organisms between sites might hide post-treatment effects, as suggested with forest soil organisms in a Finnish study (Niemelä 1999). However, in my study the data showed that pre-treatment population levels were reflected in post-treatment data. This probably resulted from the short time interval between partial cutting and sampling, as discussed above. Only strong differences caused by partial cutting would be detected. Assessing pre-disturbance population levels is therefore critical, as post-disturbance controls cannot capture these local variations.

4.3 Residual structure and management implications

Stand structure and composition can affect biodiversity, productivity (Franklin *et al.* 1989, Lieffers *et al.* 1999), and severity, duration and rate of spread of insect outbreaks (Coulson and Witter 1984; Bonan and Shugart 1989; Schowalter 1996). Therefore, studies of how stand manipulation treatments may inadvertently affect both non-target and pest species are important for preserving all species (Simberloff 1999) on different landscapes across space and time. My stand-level data at EMEND suggest that extensive logging might negatively affect populations of certain lepidopterans by changing their immediate environment but also that green-tree retention is useful, at least immediately following partial cutting, to retain many larval habitats suitable for many forest moths. In this way, perhaps, sufficient populations may be left on harvested sites to 'life-boat' forest species through a cut and regeneration cycle. However, ordinations suggested that moth assemblages moved further apart with lower amounts of residual structure and thus some species disappeared from partially cut sites. These disappearances are of concern, as they seem to consist of forest interior species and other specialist groups that play potentially important roles in ecosystem function (Chapter 2).

I believe, however, that the 'big picture' might be quite different a few years following partial harvesting. Due to their high dispersal ability, I hypothesize that most lepidopterans will recover rapidly from intermediate stand disturbance such as thinning. Lepidopteran diversity over the long-term should

even increase in partially cut stands due to an increase in plant species richness and structural diversity. My data showed that partial cutting permits the immediate survival of many species in treated stands. Certain functional groups of species (e.g. generalist and early successional plant feeders) were even favored by disturbance in 1999, probably because of stress on residual plants and the increased penetration of sunlight in partially cut stands. However, a few species may still be more vulnerable to stand modifications and underscore the precautionary importance of preserving uncut areas as sources for insect recolonisation (Spence *et al.* 1999). Ecologically sound forest practices must therefore be developed on a landscape scale to be effective at preserving all species.

On that scale, it is believed that forest interior species will be preserved as long as enough 'undisturbed habitats' remain (Angelstam 1998). However, there might never be 'enough' protected habitats representative of the entire boreal mixedwood forest due to economic and social choices (Spence 2001). Alternatives such as different green-tree retention levels might offer a reasonable solution over time. My results suggest that 50% green-tree retention might be a better immediate treatment than 20% retention because of its higher potential for preserving more species associated with closed canopy forest. However, both treatments preserved many lepidopterans and could be valid at the landscape scale to meet many management goals, depending on the surrounding forest matrix. Indeed, areas harvested using current

silvicultural practices will most likely regenerate forest stands with habitats suitable for forest Lepidoptera over time. The ultimate goal will be to achieve a balanced spatial heterogeneity between harvested areas and post-rotation age reserves, which in the fire-driven boreal region will have to move around in space. Questions remain on the appropriate proportions for each habitat but this 'managed-forest mosaic' would surely contribute to the successful conservation of Lepidoptera, and possibly other mobile organisms, and to the goal of achieving sustainable forest management.

4.4 Future research directions

In the future, the boreal mixedwood forest will experience continuing pressure from forest harvesting due to increasing economic incentives. A greater understanding of insect communities will help us to manage this forest in a way that preserves its diversity and its sustainability over time. However, many gaps in our knowledge of boreal defoliator communities make it difficult to get a clear picture of how disturbance affects them. Thus scientific recommendations to forest managers are often, by necessity, incomplete. The following gaps deserve serious attention, as they seem critical for development of interesting tools:

1. We need more biological information on non-outbreaking species and their associated predators, parasitoids, and diseases. Understanding the natural dynamics of each species is the first step in understanding community

response. This knowledge might lead, for example, to the identification of species suitable as indicators of particular habitats or ecosystem processes. Generalizations could then be provided to forest managers as a tool to assist them in their planning and in the selection of protected areas across the country (CCFM 2000). Indeed, protected areas of forest representative of all habitats need to be set aside for the survival of all species until enough is known on their habitat requirements and before their potential disappearance. The English large blue [*Maculinea arion* (L.)], for example, became extinct because his ecological needs were imperfectly understood until it was too late to act on his habitat (Pyle 2001). We can also learn from the Fennoscandian experience after many decades of intensive logging. Key habitats are now conserved for red-listed species (Hansson 2001). Moths habitat requirements could be implemented in tools like the criteria and indicators of sustainable forestry in Canada (CCFM 2000) and would thus provide additional incentives to protect specific forest habitats.

2. We also need improved ecological understanding of how disturbance impacts selected groups of lepidopterans. This could lead to increased comfort with using certain taxa as indicator groups (e.g. Geometridae, microlepidoptera). This in turn could foster development of tools to assess lepidopteran assemblages, and perhaps a larger fraction of boreal forest biodiversity, based on a few key species or to monitor environmental quality

based on these species. Application of these tools would enhance our ability to achieve sustainable forest management and biodiversity preservation.

3. Linkage between light trap catches and defoliator population sizes should be established for key forest pests. If relationships are strong, or can be improved by incorporation of covariates, they will support quick assessment of defoliator populations based on light trapping, a relatively effortless sampling method for common species compared to foliage sampling (Zandt 1994). Also, further work should quantify the relative proportions of light-trapped moths that reflect local recruitment versus immigration. Such information would support stronger inferences on stand-level dynamics.

Little is known about the long-term impacts of forest harvesting on defoliators in the boreal mixedwood forest. I have shown that there is an immediate impact of partial cutting on moths and caterpillars. The next step is to integrate these results with other studies through a long-term, multi-disciplinary framework such as the EMEND project to provide a more complete understanding of biotic communities in the boreal mixedwood ecosystem. Sustainable forest management practices can be adapted for preserving biodiversity and refined to optimize long-term productivity based on this growing knowledge.

4.5 Literature cited

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Appendix 1. Moths caught at EMEND over three years.

Family	MONA[1]	Genus and Species		Trap catch			Feeding guild[2]
				1998	1999	2000	
Hepialidae	19	*Sthenopis purpurascens* (Pack.)				1	Roots
	23	*Gazoryctra hyperborea* Mösch.		27	10	2	Roots
	31	*Korscheltellus gracilis* (Grt.)		4	2	4	Roots
Sesiidae	2533	*Albuna pyramidalis* (Wlk.)	*a*				Low plants
	2561	*Synanthedon culiciformis* (L.)	*a*				Deciduous trees
Cossidae	2676	*Acossus populi* (Wlk.)				2	Roots
Tortricidae	2769	*Pseudosciaphila duplex* (Wlsm.)		10	14		Unknown
	2900	*Retinia burkeana* (Kft.)		10	18		Unknown
	3568	*Eana argentana* (Cl.)		1	34	2	Unknown
	3637	*Choristoneura conflictana* (Wlk.)		63	1151	3263	Salicaceae
	3638	*Choristoneura fumiferana* (Morr.)		29	40	13	Conifer trees
	3664	*Archips striana* (Fern.)		1			Unknown
Pyralidae	4703	*Gesneria centuriella* (D. & S.)		3	65	8	Unknown
	4953	*Phlyctaenia coronata* (Hufn.)		224	363		Unknown
	5841	*Dioryctria abietivorella / reniculelloides*		34	53	2	Conifer trees
Drepanidae	6235	*Habrosyne scripta* Gosse		6	6		Deciduous trees
	6237	*Pseudothyatira cymatophoroides* (Gn.)		3	6		Deciduous trees
	6240	*Euthyatira pudens* (Gn.)		2	1		Low plants
	6251	*Drepana arcuata* Wlk.		40	9	4	Deciduous trees
	6252	*Drepana bilineata* (Pack.)		53	12		Deciduous trees
	6255	*Oreta rosea* (Wlk.)		5	20	18	Woody plants
Geometridae	6256	*Archiearis infans* (Mösch.)			1		Deciduous trees
	6286	*Itame brunneata* (Thunb.)		3	14	1	Deciduous trees
	6290	*Itame loricaria* (Evers.)		28	66	42	Deciduous trees
	6304	*Itame bitactata* (Wlk.)		26	72	4	Woody plants
	6321	*Epelis truncataria* (Wlk.)	*a*				Woody plants
	6330	*Semiothisa ulsterata* (Pears.)		34	4	1	Deciduous trees
	6344a	*Macaria signaria dispuncta* (Wlk.)		49	15	5	Conifer trees
	6394	*Semiothisa hebetata* (Hulst)		4	12		Salicaceae
	-	*Semiothisa* sp.				1	Unknown
	6429	*Orthofidonia exornata* (Wlk.)		143	1		Woody plants
	6570	*Aethalura intertexta* (Wlk.)		76		3	Deciduous trees
	6588	*Iridopsis larvaria* (Gn.)		34	21	2	Deciduous trees
	6597	*Ectropis crepuscularia* (D. & S.)		1109	13	3	Generalist
	6598	*Protoboarmia porcelaria* (Gn.)		2	25	9	Conifer trees
	6637	*Eufidonia convergaria* (Wlk.)	*b*				Conifer trees
	6640	*Biston betularia* (L.)		7	13	1	Generalist
	6651	*Lycia ursaria* (Wlk.)			3		Deciduous trees
	6665	*Erannis tiliaria* (Harr.)		2			Deciduous trees

6676a	*Cabera exanthemata bryantaria* Tayl.	pooled with *C.erythemaria* Gn.			Unknown
6677	*Cabera erythemaria* Gn.	232	199	50	Salicaceae
6678	*Cabera variolaria* Gn.	19	149	6	Salicaceae
6731	*Euchlaena madusaria* (Wlk.)			2	Generalist
6737	*Euchlaena tigrinaria* (Gn.)	1	2	2	Deciduous trees
6743	*Xanthotype sospeta* (Drury)		1	1	Deciduous trees
6755	*Pero morissonaria* (Hy Edw.)	1			Generalist
6796	*Campaea perlata* (Gn.)	207	132	83	Generalist
6797	*Ennomos magnaria* Gn.	59			Deciduous trees
6799	*Epirranthis substriataria* (Hulst)	98	79	23	Salicaceae
6817	*Selenia alciphearia* Wlk.	33	4	3	Deciduous trees
6819	*Metanema inatomaria* Gn.	83	41	11	Salicaceae
6820	*Metanema determinata* Wlk.	35	7	9	Salicaceae
6822	*Metarranthis duaria* (Gn.)	4			Deciduous trees
6836	*Anagoga occiduaria* (Wlk.)	115	13	11	Deciduous trees
6837	*Probole alienaria / amicaria* (H.-S.)	27	9	8	Generalist
6842	*Plagodis phlogosaria* (Gn.)	26			Deciduous trees
6863	*Caripeta divisata* Wlk.	14	14	5	Conifer trees
6885	*Besma quercivoraria* (Gn.)		1		Deciduous trees
6912	*Sicya macularia* (Harr.)	31	5	1	Generalist
6954	*Synaxis jubararia* (Hulst)	7	33		Unknown
7009	*Nematocampa resistaria* (Haw.)	78	27		Generalist
7085	*Mesothea incertata* (Wlk.)	*a*			Woody plants
7139	*Cyclophora pendulinaria* (Gn.)	59	130	18	Deciduous trees
-	*Scopula* spp.	178	166	56	Unknown
7188	*Dysstroma walkerata* (Pears.)	413	204	167	Deciduous trees
7189	*Dysstroma hersiliata* (Gn.)	4	11	7	Woody plants
7191	*Dysstroma formosa* (Hulst)		5	2	Unknown
7194	*Dysstroma brunneata* (Pack.)	3	7	2	Woody plants
7199	*Eulithis propulsata* (Wlk.)	12	9		Woody plants
7201	*Eulithis testata* (L.)	2	8		Deciduous trees
7205	*Eulithis flavibrunneata* (McD.)	47	26	8	Salicaceae
7206	*Eulithis explanata* (Wlk.)	37	7	1	Woody plants
7207	*Eulithis xylina* (Hulst)	10	10		Generalist
7210	*Eustroma semiatrata* (Hulst)	164	32	13	Low plants
7213	*Ecliptopera silaceata* (D. & S.)	73	19	7	Low plants
7216	*Plemyria georgii* Hulst	5		1	Deciduous trees
7229	*Hydriomena perfracta* Swett		1		Salicaceae
7254	*Hydriomena ruberata* (Freyer)	24	2	1	Salicaceae
7257	*Hydriomena furcata* (Thunb.)	339	124	31	Salicaceae
7270	*Protitame virginalis* (Hulst)	93	73	6	Salicaceae
7285a	*Triphosa haesitata affirmaria* (Wlk.)	4	1		Unknown
7291	*Rheumaptera undulata* (L.)		1	1	Salicaceae
7293	*Rheumaptera hastata* (L.)	pooled with *R.subhastata* (Nolcken)			Deciduous trees
7294	*Rheumaptera subhastata* (Nolcken)		1		Deciduous trees
7307	*Mesoleuca ruficillata* (Gn.)	4	2		Deciduous trees
7312	*Spargania magnoliata* Gn.	3	5	1	Low plants
7313	*Spargania luctuata* (D. & S.)	85	124	41	Low plants
7316	*Perizoma basaliata* (Wlk.)	26	44	66	Unknown
7329	*Anticlea vasiliata* Gn.	13	13	6	Woody plants
7330	*Anticlea multiferata* (Wlk.)	4			Low plants
7349	*Stamnodes topazata* (Stkr.)	*a*			Unknown

	7368	*Xanthorhoe labradorensis* (Pack.)		1	1	Woody plants
	7370	*Xanthorhoe abrasaria* (H.-S.)	60	125	76	Low plants
	7371	*Xanthorhoe iduata* (Gn.)	1	2		Unknown
	7380	*Xanthorhoe fossaria* Tayl.	2			Unknown
	7388	*Xanthorhoe ferrugata* (Cl.)	13	23	1	Low plants
	7390	*Xanthorhoe lacustrata* Gn.	7	40	9	Generalist
	-	*Xanthorhoe* spp.	58	11	7	Unknown
	7394	*Epirrhoe alternata* (Mull.)	7	28	6	Low plants
	7399	*Euphyia unangulata* (Haw.)	4	9	6	Low plants
	7408	*Zenophleps alpinata* Cass.	75	64	2	Unknown
	7423	*Hydrelia albifera* (Wlk.)			1	Low plants
	7425	*Venusia cambrica* Curt.	165	24		Deciduous trees
	7429	*Venusia pearsalli* (Dyar)	494	22		Unknown
	7430	*Trichodezia albovittata* (Gn.)	3			Low plants
	7433	*Epirrita autumnata* (Bkh.)	208	44		Generalist
	7437	*Operophtera bruceata* (Hulst)	26			Salicaceae
	7440	*Eubaphe mendica* Wlk.		3		Low plants
	-	*Eupithecia* spp.	104	158	5	Unknown
	7635	*Acasis viridata* (Pack.)	2		2	Woody plants
	7637	*Cladara limitaria* (Wlk.)	292	77	1	Conifer trees
	7639	*Cladara atroliturata* (Wlk.)	28	8		Deciduous trees
	7640	*Lobophora nivigerata* Wlk.	6	3	1	Generalist
Uraniidae	7650	*Callizia amorata* Pack.	217	96	2	Woody plants
Lasiocampidae	7687	*Phyllodesma americana* (Harr.)	241	35	10	Salicaceae
	7698	*Malacosoma disstria* Hbn.	14	217	24	Salicaceae
Saturniidae	7757	*Antheraea polyphemus* (Cram.)	3	3	1	Deciduous trees
Sphingidae	7810	*Sphinx gordius* Cram.	1		1	Generalist
	7821	*Smerinthus jamaicensis* (Drury)	15	3	14	Deciduous trees
	7822	*Smerinthus cerisyi* Kby.	1620	77	527	Salicaceae
	7853	*Hemaris thysbe* (Fab.)	*a*			Woody plants
	7893	*Hyles gallii* (Rott.)	1			Low plants
Notodontidae	7895	*Clostera albosigma* Fitch	147	17	82	Deciduous trees
	7900	*Clostera brucei* (Hy. Edw.)	38	2		Salicaceae
	7901	*Clostera apicalis* (Wlk.)	28	2	11	Deciduous trees
	7922	*Pheosia rimosa* Pack.	212	9	152	Salicaceae
	7926	*Notodonta scitipennis* Wlk.		1		Salicaceae
	7928	*Notodonta simplaria* Graef.	46	2		Salicaceae
	7931	*Gluphisia septentrionis* Wlk.	160	38	93	Salicaceae
	7934	*Gluphisia lintneri* (Grt.)	5	9	1	Salicaceae
	7935	*Gluphisia severa* Hy. Edw.	*b*			Unknown
	7939	*Furcula occidentalis* (Lint.)	87	4	5	Salicaceae
	7940	*Furcula scolopendrina* (Bdv.)		3	5	Salicaceae
	8007	*Schizura unicornis* (J.E. Smith)		4	3	Deciduous trees
Arctiidae	8037	*Gnophaela vermiculata* (Grt.)	*a*			Unknown
	8043	*Eilema bicolor* (Grt.)	18	62	42	Lichens
	8098	*Clemensia albata* Pack.			1	Lichens

	8123	*Holomelina ferruginosa* (Wlk.)		6	11	16	Low plants
	8127	*Parasemia plantaginis* (L.)	*a*				Low plants
	8128	*Dodia albertae* Dyar			1		Unknown
	8129	*Pyrrharctia isabella* (J.E. Smith)			1		Generalist
	8131	*Estigmene acrea* (Drury)		1	1		Low plants
	8137	*Spilosoma virginica* (F.)			8		Generalist
	8156	*Phragmatobia fuliginosa* (L.)	*b*				Low plants
	8158	*Phragmatobia assimilans* Wlk.		15	1	1	Generalist
	8162	*Platarctia parthenos* (Harr.)		115	1	295	Deciduous trees
	8165	*Pararctia yarrowi* (Stretch)	*a*				Unknown
	8174	*Grammia turbans* (Christoph)				1	Unknown
	8196	*Grammia parthenice* (W.Kby.)			3	1	Low plants
	8197	*Grammia virgo* (L.)			1	6	Low plants
	8198	*Grammia doris* (Bdv.)			1		Low plants
	8214	*Lophocampa maculata* Harr.		12	18		Deciduous trees
	8262	*Ctenucha virginica* (Esp.)			3	1	Grasses
Lymantriidae	8294	*Dasychira vagans* (B. & McD.)	pooled with *D.plagiata* (Wlk.)				Salicaceae
	8304	*Dasychira plagiata* (Wlk.)		9	12	19	Conifer trees
	8308	*Orgyia antiqua* (L.)	*b*				Generalist
Noctuidae	8322	*Idia americalis et al.* (Gn.)		18	30	64	Lichens
	8323?	*Idia* sp.nr. *aemula*			1		Conifer trees
	8338	*Phalaenophana pyramusalis* (Wlk.)		7	1	1	Fungus
	8340?	*Zanglognatha* sp. (*lutalba?*)		32	32		Fungus
	8356	*Chytolita petrealis* Grt.		10	4	2	Fungus
	8397	*Palthis angulalis* (Hbn.)		5	21	12	Conifer trees
	8404	*Rivula propinqualis* Gn.		153	484	46	Unknown
	8450	*Hypena atomaria* Sm.		4	4	3	Unknown
	8452	*Hypena edictalis* (Wlk.)		2	10	5	Unknown
	8461	*Hypena humuli* Harr.		5			Woody plants
	8465	*Plathypena scabra* (F.)		1			Low plants
	8555	*Scoliopteryx libatrix* (L.)		1			Salicaceae
	8731	*Euclidia cuspidea* (Hgn.)			1		Grasses
	8737	*Caenurgina distincta* (Neum.)		1	2		Unknown
	8803	*Catocala relicta* Wlk.		2			Salicaceae
	8805	*Catocala unijuga* Wlk.		3	3		Salicaceae
	8817	*Catocala briseis* Edw.	*b*				Salicaceae
	8821	*Catocala semirelicta* Grt.		4	7		Salicaceae
	8881	*Abrostola urentis* Gn.				1	Woody plants
	8896	*Diachrysia aereoides* (Grt.)		1	13		Woody plants
	8901	*Polychrysia esmeralda* (Oberth.)		27	17	11	Unknown
	8909	*Autographa rubida* Ottol.			3		Low plants
	8910	*Autographa sansoni* Dod			1		Unknown
	8911	*Autographa bimaculata* (Steph.)		2	3	1	Low plants
	8912	*Autographa mappa* (G. & R.)		3	4	3	Low plants
	8913	*Autographa pseudogamma* (Grt.)			2	10	Low plants
	8914	*Autographa californica* (Speyer)		2			Unknown
	8923	*Autographa ampla* (Wlk.)			2	1	Salicaceae
	8924	*Anagrapha falcifera* (Kby.)				3	Low plants
	8927	*Syngrapha epigaea* (Grt.)	*b*				Woody plants
	8929	*Syngrapha viridisigma* (Grt.)		10	11	3	Conifer trees

8935	*Syngrapha diasema* (Bdv.)		1	1	2	Deciduous trees
8939	*Syngrapha alias* (Ottol.)		1	6	4	Conifer trees
8942	*Syngrapha rectangula* (Kby.)			1		Conifer trees
8946	*Syngrapha microgamma* (Hbn.)		1			Woody plants
8950	*Plusia putnami* Grt.			2		Grasses
8953	*Plusia venusta* Wlk.			2		Grasses
8975	*Nycteola frigidana* (Wlk.)		16	58	4	Salicaceae
8977	*Nycteola cinereana* N. & D.		5	11	3	Salicaceae
9048	*Lithacodia albidula* (Gn.)		108	65	17	Grasses
9177	*Panthea acronyctoides* (Wlk.)		16	9	1	Conifer trees
9193	*Raphia frater* Grt.		1			Salicaceae
9206.11	*Acronicta vulpina* (Grt.)				1	Salicaceae
9207	*Acronicta innotata* Gn.			4		Deciduous trees
9212	*Acronicta grisea* Wlk.		94	69	16	Deciduous trees
9241	*Acronicta fragilis* (Gn.)	*b*				Deciduous trees
9257	*Acronicta impleta* Wlk.		5	11		Deciduous trees
9261	*Acronicta impressa* Wlk.		18	7		Generalist
9272	*Acronicta oblinita* (J.E. Sm.)		1			Generalist
9318	*Alypia langtoni* Couper	*a*				Low plants
9341	*Apamea vultuosa* (Grt.)		1			Grasses
9348	*Apamea amputatrix* (Fitch)				8	Generalist
9359	*Apamea commoda* (Wlk.)			6	18	Unknown
9365	*Apamea lateritia* auct., nec Hufn.				6	Grasses
9367.1	*Apamea cogitata* (Sm.)		6	46	123	Grasses
9369	*Apamea inficita* (Wlk.)			1	29	Unknown
9394	*Apamea contradicta* (Sm.)		1		4	Unknown
9412	*Oligia laevigata* (Sm.)				1	Unknown
9419	*Oligia mactata* (Gn.)		66	6		Low plants
9420	*Oligia illocata* (Wlk.)		71	1		Deciduous trees
9431	*Parastichtis suspecta* (Hbn.)		57	23	2	Deciduous trees
9437	*Chortodes inquinata* (Gn.)	*b*				Grasses
9439	*Chortodes basistriga* (McD.)	*b*				Unknown
9457	*Amphipoea americana* (Speyer)		2	1		Grasses
9545	*Euplexia benesimilis* McD.		6	14	5	Deciduous trees
9547	*Phlogophora periculosa* Gn.		26	68	4	Deciduous trees
9549	*Enargia decolor* (Wlk.)		385	24	1	Salicaceae
9550	*Enargia infumata* (Grt.)		107	29	3	Deciduous trees
9555	*Ipimorpha pleonectusa* Grt.		40	35		Salicaceae
9556	*Chytonix palliatricula* (Gn.)			3		Fungus
9564	*Andropolia contacta* (Wlk.)		76	35	13	Deciduous trees
9578.1	*Hyppa* sp. near *xylinoides* (Gn.)		pooled with *H.brunneicrista* Sm.			Low plants
9580	*Hyppa brunneicrista* Sm.		3	5		Unknown
9656	*Platyperigea montana* (Bremer)			35	28	Unknown
9814	*Achytonix praeacuta?* (Sm.)		5	3		Unknown
9874	*Xylena curvimacula* (Morr.)		14	112	12	Deciduous trees
9875	*Xylena thoracica* (Put.-Cram.)		2	35		Deciduous trees
9878	*Lithomoia germana* (Morr.)		6	3		Deciduous trees
9881	*Homoglaea hircina* (Morr.)			66	1	Deciduous trees
9884	*Litholomia napaea* (Morr.)		24	19	12	Generalist
9888	*Lithophane innominata* (Sm.)			8	3	Generalist
9891	*Lithophane amanda* (Sm.)	*b*				Salicaceae
9909	*Lithophane tepida* Grt.			3		Deciduous trees

9913	*Lithophane georgii* Grt.	*b*			Deciduous trees
9922	*Lithophane pexata* Grt.	1	2		Deciduous trees
9928	*Lithophane thaxteri* Grt.		1		Woody plants
9933	*Eupsilia tristigmata* (Grt.)		2		Deciduous trees
9952	*Eucirroedia pampina* (Gn.)		1		Deciduous trees
9960	*Sunira verberata* (Sm.)	9	9		Unknown
9962	*Anathix puta* (G. & R.)	56	11	1	Salicaceae
9965?	*Xanthia* sp.nr. *togata*		1		Salicaceae
9967	*Hillia iris* (Zett.)	16	11	2	Salicaceae
9976	*Platypolia anceps* (Steph.)	288	10		Low plants
9980	*Xylotype acadia* B. & Benj.	91	17		Generalist
9987?	*Mniotype* sp. (*ducta?*)	3	1		Unknown
9990	*Sutyna profunda* (Sm.)	5	1		Unknown
9993	*Brachylomia populi* (Stkr.)	1			Salicaceae
9998	*Brachylomia algens* (Grt.)	56	4		Salicaceae
9999	*Brachylomia discinigra* (Wlk.)	42			Unknown
10005	*Feralia jocosa* (Gn.)	pooled with *F.comstocki* Grt.			Conifer trees
10008	*Feralia comstocki* Grt.	31	39	2	Conifer trees
10055	*Apharetra dentata* (Grt.)		1		Woody plants
10059	*Homohadena badistriga* (Grt.)		3		Woody plants
10197	*Cucullia florea* Gn.			2	Low plants
10275	*Polia nimbosa* (Gn.)	37	84	51	Generalist
10277	*Polia rogenhoferi* (Mösch.)	2	4	1	Unknown
10278	*Polia propodea* McCabe			1	Unknown
10280	*Polia purpurissata* (Grt.)		14	8	Generalist
10292	*Melanchra adjuncta* (Gn.)	2	7		Generalist
10297	*Lacanobia atlantica* (Grt.)		2		Generalist
10298	*Lacanobia radix* (Wlk.)	23	19	7	Generalist
10303	*Trichordestra tacoma* (Strecker)			1	Generalist
10310	*Papestra quadrata* (Sm.)			1	Generalist
10312	*Papestra cristifera* (Wlk.)	1			Generalist
10315	*Anartomina secedens* (Wlk.)	2	6	6	Woody plants
10397	*Lacinipolia renigera* (Steph.)			2	Generalist
10405	*Lacinipolia lorea* (Gn.)	4	19	21	Low plants
10406	*Lacinipolia olivacea* (Morr.)		2	1	Low plants
10436	*Aletia oxygala* (Grt.)	1	16	3	Grasses
10446	*Leucania multilinea* Wlk.		1		Low plants
10449	*Leucania insueta* Gn.	1	2	4	Grasses
10471	*Stretchia plusiaeformis* Hy. Edw.		1	4	Woody plants
10490	*Orthosia revicta* (Morr.)	70	144	9	Generalist
10493	*Orthosia segregata* (Sm.)	51	61	3	Woody plants
10495	*Orthosia hibisci* (Gn.)	32	57	1	Deciduous trees
10513	*Egira dolosa* (Grt.)	1			Salicaceae
10524	*Nephelodes minians* Gn.	1	16		Grasses
10563	*Protorthodes oviduca* (Gn.)			6	Low plants
10641	*Agrotis vetusta* (Wlk.)	*b*			Woody plants
10651	*Agrotis venerabilis* Wlk.			2	Low plants
10670	*Feltia jaculifera* (Gn.)			1	Low plants
10676	*Feltia herilis* (Grt.)		4	1	Low plants
10702	*Euxoa divergens* (Wlk.)		1	12	Unknown
10756	*Euxoa campestris* (Grt.)			1	Woody plants
10801	*Euxoa ochrogaster* (Gn.)	*b*			Low plants

10825.1	*Euxoa castanea* Laf.		1	2	Low plants
10861	*Euxoa ridingsiana* (Grt.)	*b*			Unknown
10891	*Ochropleura implecta* Laf.		3	1	Low plants
10918	*Diarsia dislocata* (Sm.)	55	222	305	Unknown
10921	*Diarsia rosaria* (Grt.)	20	1	7	Low plants
10926	*Spaelotis clandestina* (Harr.)			1	Generalist
10928	*Graphiphora augur* F.	17	34	17	Deciduous trees
10929	*Eurois occulta* (L.)	124	103	74	Deciduous trees
10930	*Eurois astricta* Morr.	179	297	154	Salicaceae
10942	*Xestia c-nigrum* (L.)	1		1	Generalist
10943	*Xestia normaniana* (Grt.)		2		Woody plants
10944	*Xestia smithii* (Snell.)	36	39	24	Generalist
10947	*Xestia oblata* (Morr.)	1	12	5	Salicaceae
10954	*Agnorisma bugrai* Koçak	1	5		Woody plants
10958	*Xestia fabulosa* (Fgn.)	2	2	2	Woody plants
10959,1	*Xestia mixta* (Wlk.)	205	35	94	Woody plants
10962	*Xestia perquiritata* (Morr.)	59	17	1	Conifer trees
10964	*Xestia homogena* McD.	85	20	36	Unknown
10965	*Xestia imperita* (Hbn.)		13	1	Conifer trees
-	*Xestia* sp.			1	Unknown
10992	*Paradiarsia littoralis* (Pack.)		4	8	Deciduous trees
10996	*Cerastis salicarum* (Wlk.)	33	107	6	Unknown
10999	*Aplectoides condita* (Gn.)	71	40	11	Conifer trees
11000	*Anaplectoides prasina* (D. & S.)	2	21	8	Generalist
11001	*Anaplectoides pressus* (Grt.)	14	114	81	Generalist
11003	*Chersotis juncta* (Grt.)		1		Low plants
11004	*Protolampra rufipectus* (Morr.)	1	51	105	Generalist
11008	*Eueretagrotis perattanta* (Grt.)		3	5	Woody plants
11012	*Cryptocala acadiensis* (Bethune)		9	7	Woody plants
11041	*Abagrotis placida* (Grt.)		8	4	Generalist
11051	*Ufeus satyricus* Grt.	7			Salicaceae
11064	*Pyrrhia exprimens* (Wlk.)	1	1		Woody plants

1 – MONA numbers from Hodges, R.W. *et al.* 1983. Check List of the Lepidoptera of America North of Mexico.

2 – Refer to Chapter 2 for details on feeding guild classification.

a – Species caught by diurnal netting.

b – Species caught by light trapping at the sheet.